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Anuran Amphibians from the Cordillera de Huancabamba, Northern Peru: Systematics, Ecology, and Biogeography

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ABSTRACT The anuran fauna of the Cordillera de Huancabamba in northern Peru consists of 21 species, 10 of which are endemic. Most of the species and all of the endemics occur in the humid montane forest on the western slope and summit of the cordillera, where most of the species are eleutherodactylines that have direct development of terrestrial eggs. Only five species occur in the dry tropical forest at elevations below 1700 m in the cordillera. Seven groups are recognized based on ecological similarity. Eight species reach the southern limits of their distributions in the cordillera, and one species reaches its northern limit. *Centrolene buckleyi*, *Eleutherodactylus cryptomelas*, and *E. phoxocephalus* are reported for the first time from Peru. *Eleutherodactylus ceuthospilus*, *E. rhodoplichus*, *E. sternothylax*, and *E. wiensi* are described as new species. *Colostethus paradoxus* and *Phyllobates anthonyi* are placed in the synonymy of *Epipedobates tricolor*. The tadpole of *Colostethus sylvaticus* is described.

Key words: Peru, Andes, Biogeography, Ecological distribution, Anura, New species.

RESUMEN La fauna de anuros de la Cordillera de Huancabamba en el norte del Perú consiste de 21 especies, 10 de las cuales son endémicas. La mayoría de las especies y el total de las endémicas ocurren en el bosque húmedo de montaña en la ladera occidental y en lo alto de la cordillera, donde la mayoría de las especies son

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eleutherodactílinos que tienen desarrollo directo de huevos terrestres. Solamente cinco especies ocurren en el bosque seco tropical en elevaciones bajo los 1700 m en la cordillera. Se reconocen siete grupos basados en similitud ecologica. Ocho especies alcanzan los limites australes de sus distribuciones en la cordillera, y una especie alcanza su limite septentrional. *Centrolene buckleyi*, *Eleutherodactylus cryptomelas*, y *E. phoxocephalus* se reportan por primera vez del Perú. *Eleutherodactylus ceuthospilus*, *E. rhodoplichus*, *E. sternothylax*, y *E. wiensi* se describen como especies nuevas. *Colostethus paradoxus* y *Phyllobates anthonyi* se ponen en la sinonimia de *Epipedobates tricolor*. Se describe el renacuajo de *Colostethus sylvaticus*.

Palabras claves: Peru, Los Andes, Biogeografia, Distribución ecológica, Anura, especies nuevas.

The major physiographic feature in western South America is the Andes, a nearly unbroken mountain chain that extends for about 8000 km from Venezuela to the southern tip of the continent. Most passes in the tropical Andes are at elevations above treeline, but there are two exceptions. In western Venezuela, a major break, the Cúcuta Depression at an elevation of about 600 m, separates the Venezuelan or Mérida Andes from the Cordillera Oriental of the principal Andean chain. The second break, the Huancabamba Depression, is far more complex. This region is a complex of relatively low ridges and basins in northern Peru and extreme southern Ecuador. In the Huancabamba Depression, the lowest pass between Pacific and Atlantic drainages is the Abra de Porculla at 2145 m in northern Peru. This major interruption of the Andean chain has biogeographic significance, which was discussed in relation to Andean plants by Simpson (1975), the herpetofauna by Duellman (1979), and to the avifauna by Vuilleumier (1969) and by Parker et al. (1985).

Herpetological collections were made along a transect across the Cordillera de Huancabamba in the Huancabamba Depression by three field parties from The University of Kansas in 1970, 1979, and 1991, and by a field party from Louisiana State University in 1974. These combined collections contain 21 species of anurans, nine of which were new to science—*Gastrotheca galeata* (Trueb and Duellman, 1978), *Gastrotheca lateonota* (Duellman and Trueb, 1988), *Phrynopus nebulanastes* (Cannatella, 1984), *Phrynopus parkeri* (Lynch, 1975), *Phyllonastes heyeri* (Lynch, 1986), and four species of *Eleutherodactylus* named herein.

The collections from the Cordillera de Huancabamba are the most extensive for any of the highland regions in the middle of the depression and therefore are significant to our understanding of the transitional nature of the fauna between the northern and central Andes. The purposes of this paper are to: (1) describe four new species of leptodactylid frogs of the genus *Eleutherodactylus*, (2) report on the occurrence of 17 other species

of anurans from the cordillera, (3) summarize data on the ecological distribution of the anurans in the cordillera, and (4) provide a biogeographic synthesis of the anuran fauna.

MATERIALS AND METHODS

In addition to specimens in the Museum of Natural History, The University of Kansas (KU), we have examined specimens in the Florida Museum of Natural History (UF); Museum of Comparative Zoology, Harvard University (MCZ); Museum of Natural Sciences, Louisiana State University (LSUMZ); and the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MHNSM) in Lima, Peru. Measurements of *Eleutherodactylus* were taken in the manner described by Lynch and Duellman (1980) and the numbered diagnoses follow the format used therein. The designation of species groups of *Eleutherodactylus* follows Lynch (1976). In the diagnoses of *Eleutherodactylus*, comparisons are made only with other species from southern Ecuador, Amazonian slopes of the Andes of Ecuador, and Andean Peru. In the descriptions of species, the following abbreviations are used: ED = longitudinal diameter of eye, E–N = eye nostril distance, EW = greatest width of eyelid, FL = foot length, HL = head length, HW = head width, IOD = interorbital distance, SVL = snout-vent length, TL = tibia length; TYM = tympanum length. Tadpoles were staged according to Gosner (1960). The labial tooth row formula in tadpoles is abbreviated LTRF. All measurements and proportions are given as ranges and means; one standard deviation of the mean is given for samples of 10 or more individuals. Measurements are given separately for males and females; proportions are combined unless there are significant differences between the sexes.

Terminology of vegetation types is that of the Holdridge system as applied to Peru by Tosi (1960). Ecological data were analyzed using Cluster Analysis of Cases, with species as cases, of the BMDP software (Dixon, 1981); this clustering program generates phenograms based on distance measures, thereby illustrating similarities among cases.

THE HUANCABAMBA DEPRESSION

In the Huancabamba Depression, the major north-south cordilleras are fragmented into isolated ranges usually less than 3500 m high that are separated by valleys mostly between 1000 and 2000 m above sea level (Fig. 1). Several small rivers drain the Pacific slopes, but east of the continental divide, all streams eventually drain into the Río Marañón, a major tributary of the Río Amazonas. The interior basins are dry and support dry forest dominated by legumes and cacti; the tops of the ridges above 3000 m and the

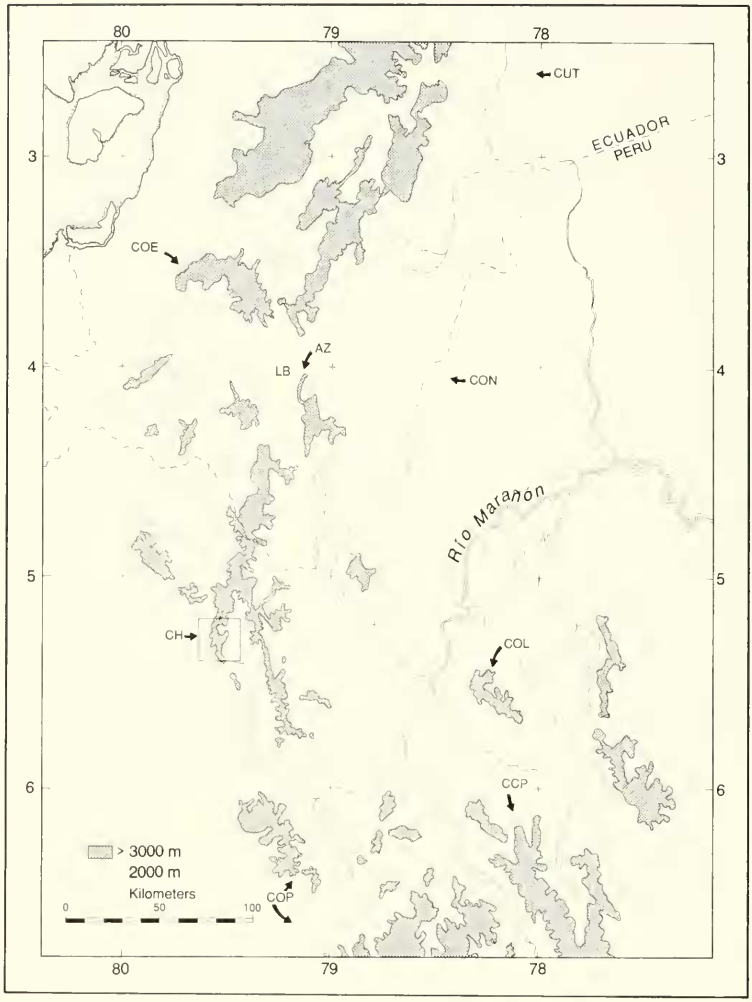

Fig. 1. Map of Huancabamba Depression. Square indicates area shown in detail in Figure 2. AZ = Abra de Zamora, Ecuador; CCP = Cordillera Central, Peru; CH = Cordillera de Huancabamba, Peru; COE = Cordillera Occidental, Ecuador; COL = Cordillera Colán, Peru; CON = Cordillera del Cóndor, Ecuador; COP = Cordillera de Occidental, Peru; CUT = Cordillera de Cutucú, Ecuador; LB = Loja Basin, Ecuador.

upper western slopes are relatively wet and support cloud forest.

At the Huancabamba Depression there is a structural deflection of the Andean faults that separate two major tectonic segments of the Andes (Sillitoe, 1974). To the south of the depression, the axis of the Andes is northwest to southeast, whereas to the north of the depression, the axis is north-northeast to south-southwest. According to Ham and Herrera (1963), the region that is now the Huancabamba Depression had extensive marine transgressions in the Cretaceous. The major uplift of the Andes to the south of the depression was in the Miocene (Harrington, 1962; Aubodin et al., 1973); the final major uplift was completed in the Pliocene with some additional orogeny in the Pleistocene (James, 1973; Gansser, 1973). The Andes to the north of the depression probably had few areas above 1000 m above sea level in the early Pliocene; the major orogeny occurred at the end of the Pliocene with uplift continuing through the Pleistocene (Herd and Naeser, 1974; Shagam, 1975; Simpson, 1979). Thus, the Huancabamba Depression is not only a tectonic boundary but bridges tectonic segments that were uplifted at different times.

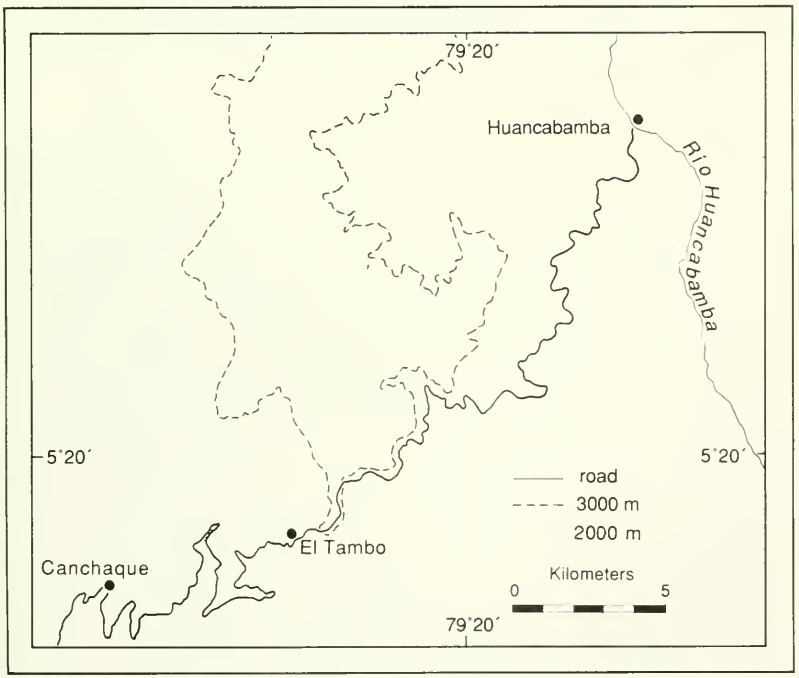

Fig. 2. Map of location of transect across the Cordillera de Huancabamba.

Fig. 3. Partially cleared tropical dry forest 8.4 km west of Canchaque; valley is at an elevation of 620 m. January 1991.

Fig. 4. Partially cleared upper humid montane forest at 3010 m on upper eastern slope of Cordillera de Huancabamba. February 1979.

Fig. 5. Bromeliad laden tree in upper humid montane forest at 3010 m on upper eastern slope of Cordillera de Huancabamba. February 1979.

Fig. 6. Clouds spilling over crest from western slope of Cordillera de Huancabamba. February 1979.

According to Harrington (1956) and Gansser (1973), the present elevations and drainage patterns in the Huancabamba Depression probably were attained in the Pleistocene. Climatic fluctuation in the Pleistocene brought about cooler and drier conditions during glacial phases and warmer and more moist conditions during interglacial phases. Climates were depressed 1500–2000 m in the Ecuadorian Andes (Sauer, 1971) and in the Peruvian Andes, 1000–1500 m on the eastern slopes and 500–1000 m on the western slopes (Hastenrath, 1967; Dollfus, 1976). These climatic fluctuations presumably resulted in alternating corridors for, and barriers to, dispersal in the high Andes (Simpson, 1979).

The Cordillera de Huancabamba is a north-south ridge in the central part of the Huancabamba Depression. The transect is a dirt road that extends 70 km roughly east–northeast from the village of Canchaque (1120 m), over the crest of the cordillera at 3110 m, and down to the town of Huancabamba at 1840 m (Fig. 2). From Canchaque to an elevation of about 1700, the vegetation is tropical dry forest, much of which has been cleared for agriculture and pasture (Fig. 3). Above 1700 m on the western slope, humid montane forest prevails; by 3000 m, the trees are dwarfed and there is a great amount of moss and numerous arboreal and terrestrial bromeliads (Figs. 4, 5). The upper western slopes frequently are bathed in fog and receive much more rain than the lower slopes (Fig. 6). The eastern slopes are dramatically drier; tropical dry forest extends from the Huancabamba Valley, which is extensively cultivated, to nearly 3000 m on the eastern slopes of the Cordillera de Huancabamba.

DESCRIPTIONS OF NEW SPECIES

Eleutherodactylus ceuthospilus new species

Holotype.—KU 219775, an adult male from the west slope of the Cordillera de Huancabamba, 15.8 km (by road) ENE of Canchaque (05°23'S, 79°34'W, 1800 m), Provincia Huancabamba, Departamento Piura, Peru; one of a series collected on 7 January 1991 by Fernando M. Cuadros, John J. Wiens, and Erik R. Wild.

Paratypes.—KU 219776–82 and MHNSM 15387–94 collected with the holotype; KU 219783–84 and MHNSM 15395–97 from 16 km (by road) ENE of Canchaque, 1840 m; KU 181270, 181272–78, 196492–98, LSUMZ 32321–31 from 15 km (by road) ENE of Canchaque, 1735 m; all Departamento Piura, Peru.

Referred specimens.—KU 219785, a subadult female, from the type locality; KU 212215–18, adult males from 12 km W of Lamas, 1500 m, Departamento Cajamarca, Peru.

Diagnosis.—A member of the *Eleutherodactylus unistrigatus* group characterized by: (1) skin of dorsum shagreened with minute, low, round

tubercles and lacking folds; skin on venter granular; (2) tympanum distinct, round, diameter about half that of eye; separated from eye by distance slightly less than diameter of tympanum; (3) snout acutely rounded in dorsal view and in profile and barely protruding; canthus rostralis rounded; (4) upper eyelid narrower than interorbital distance and lacking tubercles; cranial crests absent; (5) vomerine odontophores low, concealed in buccal mucosa; (6) males with large, median, subgular vocal sac; vocal slits present; nuptial excrescences absent; (7) first finger shorter than second; pads large, elliptical, nearly truncate; pad on Finger III equal to or slightly broader than length of tympanum; (8) fingers with lateral keels; (9) few low, diffuse ulnar tubercles; (10) no tubercles on heel; outer edge of tarsus with few low, round tubercles; inner edge of tarsus with low tubercles, occasionally coalesced into a fold; (11) two metatarsal tubercles; inner large, ovoid, at least six times size of subconical outer tubercle; many low, minute supernumerary plantar tubercles; (12) toes with lateral keels, lacking webbing; pads equal to or slightly smaller than those on fingers; (13) dorsum gray to pale brown, usually with small brown flecks or streaks; flanks cream; narrow dark brown canthal and supratympanic stripes and interorbital and labial bars; posterior surfaces of thighs brown with cream (orange or yellow in life) spots (also spots in groin); venter cream with minute dark flecks; (14) adults small, 35 males 19.0–25.8 mm SVL, eight females 23.5–26.7 mm SVL.

Of the other species in the *Eleutherodactylus unistrigatus* group in Peru and southern Ecuador having concealed vomerine odontophores, *E. mendax* differs by its larger size (males to 27.8 mm), bluntly rounded snout, more tuberculate dorsal skin, conical tubercles on the heel, and smaller, rounded pads. Both *E. colodactylus* (males from Cordillera de Huancabamba to 20.0 mm, females to 20.7 mm) and *E. salaputium* (males to 18.6 mm) are slightly smaller and lack yellow spots in the groin and on the posterior surfaces of the thighs. Moreover, *E. colodactylus* has a subacuminate snout and small hands and feet with relatively small, round pads, whereas *E. salaputium* has a more tuberculate dorsum, subconical tubercles on the heel, and dark venter. *Eleutherodactylus rhodoplichus*, which occurs at higher elevations in the Cordillera de Huancabamba, lacks vomerine teeth (at least in males), is larger (males to 28.9 mm, females to 34.2 mm) than *E. ceuthospilus*, has a subacuminate snout, distinct tarsal fold, and rose-red (instead of yellow or orange) in the groin and on the posterior surfaces of the thighs.

Description.—Thirty-five adult males, eight adult females. Head as wide as body, as long as wide; HW 31–39% ($\bar{x}$ = 35 ± 2) of SVL; HL 32–39% ($\bar{x}$ = 35 ± 2) of SVL; snout moderately long, slightly protruding beyond margin of lip; acutely round in dorsal view and in profile; E–N equal to ED; E-N 23–33% ($\bar{x}$ = 27 ± 2) of HL; eye moderately large, ED

24–35% ($\bar{x}$ = 29 ± 3) of HL; upper eyelid smooth, EW 53–93% ($\bar{x}$ = 71 ± 9) of IOD. Top of head flat; cranial crests absent; canthus rostralis shallowly sigmoid, rounded; loreal region concave; lip barely flared anterior to orbit; internarial area not depressed; nostril ovoid, distinctly protruding laterally at point above anterior margin of lower jaw. Supratympanic fold weak, curving posteroventrally from posterior corner of orbit, usually obscuring dorsal and posterodorsal parts of tympanic annulus; tympanum round, separated from eye by distance equal to or slightly less than TYM, which is 43–68% ($\bar{x}$ = 51 ± 6) of ED. Choanae small, round, widely separated, not obscured by palatal shelf of maxillary arch; vomerine odontophores concealed; 1–3 teeth protruding through buccal mucosa posteromedialy to choanae in some specimens. Tongue elliptical, shallowly notched posteriorly, free behind for about one fourth of its length; vocal slit elongate, extending from midlateral base of tongue toward angle of jaws; vocal sac large, single, median, subgular.

Skin on dorsum of head, body, and limbs, and on flanks shagreened with minute round tubercles; dermal folds absent on dorsum; belly and ventral surfaces of thighs granular; other ventral surfaces smooth; discoidal fold evident; three to six diffuse ulnar tubercles, heel lacking tubercles; three to four low, diffuse tubercles on outer edge of tarsus. Cloacal opening unmodified, directed posteriorly at upper level of thighs.

Forearm slender; fingers moderately short, slender, bearing narrow, lateral keels and broad, elliptical, nearly truncate discs; disc on Finger I noticeably smaller than those on other fingers; relative lengths of Fingers I < II < IV < III; subarticular tubercles large, round to subconical; supernumerary tubercles basally on Fingers III and IV; palmar tubercle slightly elevated, distinctly bifid; thenar tubercle elliptical, slightly elevated (Fig. 7); males lacking nuptial excrescences. Hind limbs moderately robust; heels barely overlapping when hind limbs flexed at right angles to axis of body; TL 44–52% ($\bar{x}$ = 48 ± 2) of SVL; FL 36–51% ($\bar{x}$ = 43 ± 3) of SVL. Row of low tubercles on inner edge of tarsus, in some specimens coalesced on distal half of tarsus to form low fold; inner metatarsal tubercle large, ovoid; outer metatarsal tubercle small, subconical; toes moderately long, slender, unwebbed, bearing narrow lateral keels and elliptical discs nearly as large as those on fingers; relative lengths of toes I < II < III < V < IV; subarticular tubercles small, round; supernumerary tubercles minute, only on proximal segments of digits (Fig. 7).

Color in preservative (including one subadult female): Dorsum of head, body, and limbs gray to pale brown, lacking markings except for diffuse brown interorbital-occipital mark (12 individuals), or with dorsal pattern consisting of dark brown flecks or longitudinal dashes (19); irregular dark brown markings and narrow, pale middorsal line (2); pale middorsal area narrowly bordered by dark brown (2); broad, pale, dorsolateral stripes

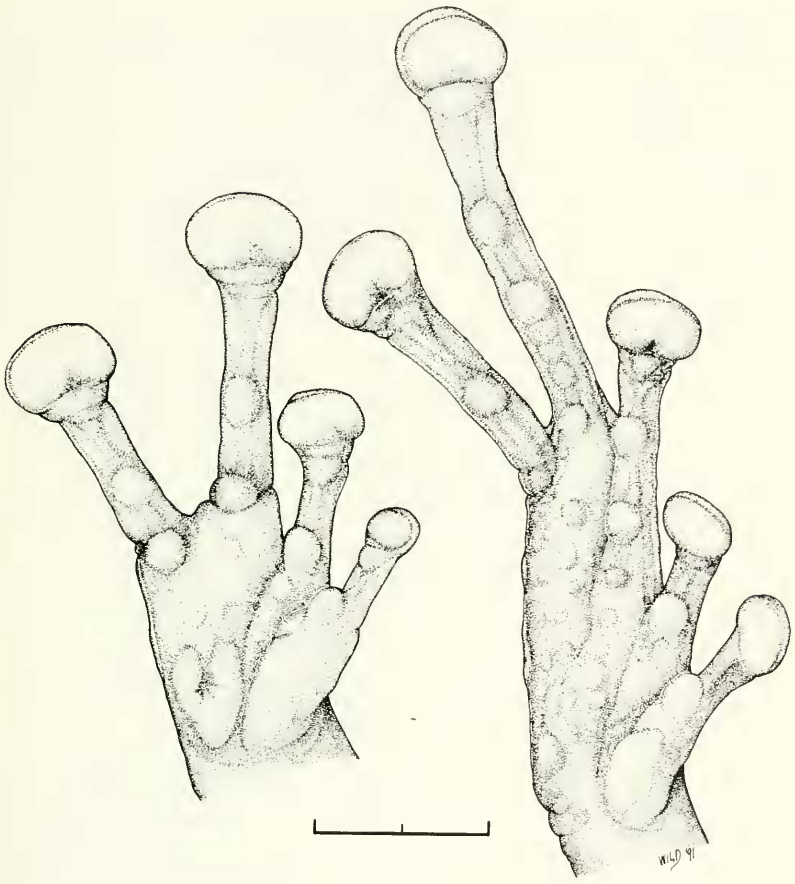

Fig. 7. Hand and foot of holotype of *Eleutherodactylus ceuthospilus*, KU 219775. Scale = 2 mm.

bordered by dark brown (2), or two medial pale spots narrowly bordered by dark brown. Flanks cream to tan. Unpatterned individuals usually lacking distinct bars on limbs; bars on limbs usually distinct in other individuals—1 or 2 on forearm, 2 or 3 on thigh and shank, 1 or 2 on tarsus. Narrow brown canthal and supratympanic stripe; diffuse suborbital bars on lip in some individuals. Groin and posterior surfaces of thighs cream to pale orange; posterior surfaces of thighs with dark brown reticulations. Venter cream with minute brown flecks.

Color in life: KU 219775: dorsum brown medially and pale tan laterally onto flanks and to tip of snout; dark brown supratympanic mark; small yellow and orange spot in axilla; vocal sac bright yellow; rest of venter

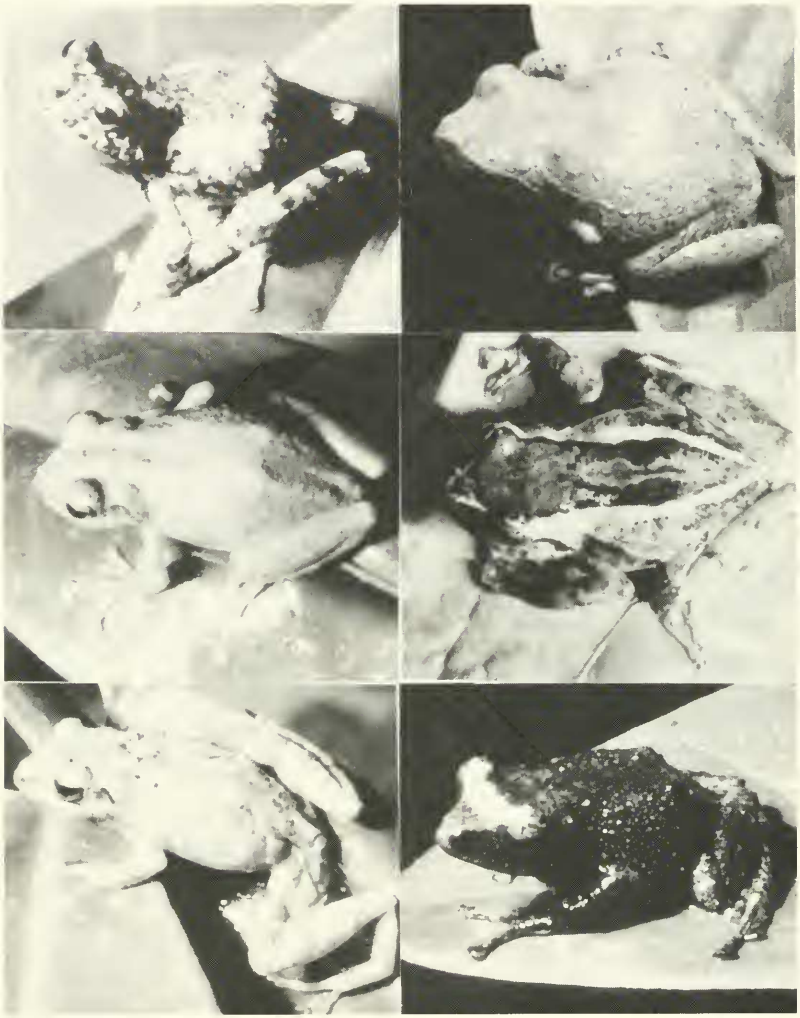

Fig. 8. **Left:** *Eleutherodactylus ceuthospilus*—**Top,** KU 219775, male, 20.4 mm SVL; **middle,** KU 219776, male, 22.2 mm SVL; **bottom,** KU 219777, subadult female, 22.0 mm SVL. **Right:** *Eleutherodactylus rhodoplichus*—**Top,** KU 219786, male, 27.6 mm SVL; **middle,** KU 219791, subadult female, 28.7 mm SVL; **bottom,** KU 219787, male, 25.7 mm SVL.

transparent yellow (Fig. 8). KU 219776: dorsum uniform yellowish olive; vocal sac bright yellow, rest of venter yellowish white (Fig. 8). KU 219777: dorsum tan with two median creamy-white spots narrowly bordered by brown (Fig. 8). In all specimens, inguinal region and posterior surfaces of thighs with bright yellow to orange spots; iris reticulated with gold (E. R.

Wild field notes, 7 January 1991). KU 196492–95: dorsum gray to tan or medium brown with faint darker markings; posterior surfaces of thighs marbled with orange (R. Thomas field notes, 8 December 1974).

Measurements (in mm; 35 males, followed by 8 females): SVL 19.0–25.8 (21.3 ± 1.51), 23.5–26.7 (25.2 ± 1.29); TL 9.2–12.4 (10.4 ± 0.79), 11.1–13.0 (11.9 ± 0.68); FL 7.3–11.8 (9.3 ± 1.05), 9.1–11.3 (10.3 ± 0.65); HW 6.2–10.0 (7.4 ± 0.82), 7.9–9.1 (8.6 ± 0.44); HL 6.7–9.3 (7.6 ± 0.63), 8.3–9.3 (8.8 ± 0.40); IOD 2.2–2.8 (2.5 ± 0.16), 2.7–3.1 (2.9 ± 0.14); EW 1.4–2.5 (1.8 ± 0.25), 1.6–2.4 (2.0 ± 0.27); E–N 1.7–2.7 (2.1 ± 0.25), 1.9–2.7 (2.3 ± 0.24); ED 1.7–3.0 (2.2 ± 0.30), 2.3–2.6 (2.5 ± 0.09); TYM 0.9–1.3 (1.1 ± 0.10), 1.1–1.5 (1.3 ± 0.13).

Distribution and ecology.—*Eleutherodactylus ceuthospilus* is known from elevations of 1735–1840 m in humid montane forest on the western slopes of the Cordillera de Huancabamba and at 1500 m at a site 12 km W of Lamas on the Pacific slopes of the Cordillera Occidental in northern Peru. At 15 km ENE of Canchaque on the night of 8 December 1974, Richard Thomas found males calling from leaves and stems of herbaceous vegetation 15–40 cm above the ground along a roadcut in cloud forest. Males also were calling at night from low vegetation at 15.8 km ENE of Canchaque on 7 January 1991. Adults of both sexes were found in bromeliads by day on 5 and 6 December 1974 at 15 km ENE of Canchaque. The call is a ratchetlike, rapid sequence of three clicks (rarely 2 or 4) repeated at intervals of 15–20 sec (R. Thomas, field notes, 8 December 1974).

Etymology.—The specific name is derived from the Greek *keuthos* meaning hidden and the Greek *spilos* meaning spot; the name alludes to the yellow spots in the groin and anterior and posterior surfaces of thighs that are hidden when the frog is in a sitting position.

Eleutherodactylus rhodoplichus new species

Holotype.—KU 219786, an adult male, from El Tambo, 31 km (by road) ENE of Canchaque, west slope of the Cordillera de Huancabamba (05°22'S, 79°33'W, 2770 m), Provincia Huancabamba, Departamento Piura, Peru; one of a series collected on 8 January 1991 by Fernando M. Cuadros, John J. Wiens, and Erik R. Wild.

Paratypes.—KU 219787–90 and MHNSM 15400–04 collected with the holotype; KU 196499–503 and LSUMZ 32428–33 from near the crest of Cordillera de Huancabamba, 33 km (by road) SW of Huancabamba, 3050 m, Departamento Piura, Peru.

Referred specimens.—KU 219791 from the type locality; LSUMZ 32417 (same data as LSUMZ 32428–33); and KU 219792 from 12.7 km (by road) NE of El Tambo, 2820 m, Departamento Piura, Peru; all subadult females.

Diagnosis.—A member of the *Eleutherodactylus unistrigatus* group characterized by: (1) skin of dorsum coarsely shagreened with scattered low, round to subconical tubercles and lacking folds; skin on venter granular; (2) tympanum distinct, round, diameter about 30–60% that of eye, separated from eye by distance equal to or slightly less than diameter of tympanum; (3) snout subacuminate in dorsal view, rounded in profile, barely protruding; canthus rostralis curved, rounded; (4) upper eyelid narrower than interorbital distance with few, low, round, diffuse tubercles; cranial crests absent; (5) vomerine odontophores usually absent (present in some females); (6) males with large, median, subgular vocal sac posterior onto throat, vocal slits present, nuptial excrescences absent; (7) first finger shorter than second; pads large, elliptical, nearly truncate; pad on Finger III about one and one-half times diameter of tympanum; (8) fingers bearing lateral keels; (9) few low ulnar tubercles; (10) several small subconical tubercles on heel; outer edge of tarsus with round, diffuse tubercles, inner edge with low fold; (11) two metatarsal tubercles; inner large, elliptical, three times size of round, conical outer tubercle; many low, round supernumerary plantar tubercles; (12) toes bearing lateral fringes, lacking webbing; pads slightly smaller than those on fingers; (13) dorsum brown, with fine, irregular darker brown markings (pale transverse bar on head or dorsolateral stripes usually absent) including narrow supratympanic stripe, interorbital triangular mark, and diffuse canthal stripe; flanks pale brown with darker brown reticulations or diagonal streaks; venter cream to tan with dark brown flecks; posterior surfaces of thighs creamy tan with brown reticulations; (14) adults moderately sized, seventeen males 21.8–28.9 mm SVL, four females 30.1–34.2 mm SVL.

Eleutherodactylus rhodoplichus is compared with other species of the *E. unistrigatus* group in Peru and Ecuador that have a tarsal fold and lack vomerine teeth in males. Of these, *E. mendax* has a bluntly rounded snout in dorsal view and a unicolor venter; *E. incomptus* has a less acuminate snout, a row of tarsal tubercles instead of a distinct fold, uniformly brown posterior surfaces of the thighs, and much smaller size (males to 18.8 mm, females to 25.9 mm).

Description.—Seventeen adult males, four adult females. Head not as wide as body, slightly longer than wide; HW 32–42% ($\bar{x} = 37 \pm 2$) of SVL; HL 33–39% ($\bar{x} = 36 \pm 2$) of SVL; snout moderately long, protruding beyond margin of lip, acuminate in dorsal view, acutely rounded in profile; E-N slightly less than ED; E–N 22–28% ($\bar{x} = 25 \pm 2$) of HL; eye moderately large, ED 23–37% ($\bar{x} = 30 \pm 3$) of HL; upper eyelid bearing numerous small, low tubercles, EW 52–90% ($\bar{x} = 76 \pm 9$) of IOD. Top of head flat; cranial crests absent; canthus rostralis slightly curved, rounded; loreal region slightly concave; lip barely flared anterior to orbit; internarial area depressed; nostril ovoid, slightly protruding laterally at point just posterior

to anterior margin of lower jaw. Supratympanic fold weak, curving posteroventrally from posterior corner of orbit, barely obscuring dorsal and posterodorsal parts of tympanic annulus; tympanum round, separated from eye by distance less than TYM, which is 32–61% ($\bar{x}$ = 42 ± 7) of ED. Choanae small, round, widely separated, not obscured by palatal shelf of maxillary arch; vomerine odontophores absent in males and most females; in two females, odontophores small, elliptical, widely separated medially, transverse, at level behind posterior margins of choanae, each bearing 0–3 ($\bar{x}$ = 1.2) teeth. Tongue elliptical, shallowly notched posteriorly, free behind for about one-third of its length; vocal slit elongate, extending from midlateral base of tongue toward angle of jaws; vocal sac large, single, median, subgular, extending onto chest.

Skin of dorsum coarsely shagreened with numerous low, round to subconical tubercles more or less evenly distributed on head and body and less numerous and diffuse on dorsal surfaces of limbs; skin on flanks smooth to weakly areolate; belly and ventral surfaces of thighs granular; other ventral surfaces smooth; discoidal fold distinct; short, low, longitudinal dorsolateral fold evident in scapular region in some individuals; four to six distinct ulnar tubercles, one moderately large and several small tubercles on heel; row of low tubercles on outer edge of tarsus. Cloacal opening unmodified, directed posteroventrally at upper level of thighs, bordered below by numerous small tubercles.

Forearm moderately robust; fingers moderately short, slender, bearing narrow lateral keels and broad, elliptical, nearly truncate discs, widest on Fingers III and IV; relative lengths of fingers I < II < IV < III; subarticular tubercles large, round, elevated; supernumerary tubercles basally on Fingers II–IV; palmar tubercle elevated, triangular, trifid (three separate tubercles in some individuals); thenar tubercle broadly ovoid, slightly elevated (Fig. 9); males lacking nuptial excrescences. Hind limbs moderately robust, long; heels barely overlapping when hind limbs flexed at right angles to axis of body; TL 42–56% ($\bar{x}$ = 50 ± 3) of SVL; FL 43–54% ($\bar{x}$ = 49 ± 3) of SVL. Tarsal fold on at least distal two thirds of tarsus; inner metatarsal tubercle large, elliptical; outer metatarsal tubercle small, round; toes long, slender, unwebbed, bearing narrow lateral keels and elliptical discs slightly smaller than those on fingers; relative lengths of toes I < II < III < V < IV; subarticular tubercles small, round to subconical; supernumerary tubercles low, diffuse on proximal segments of digits (Fig. 9).

Color in preservative: Dorsum of head, body, and limbs in three females and 11 males brown with dark brown markings consisting of diffuse interorbital triangle with apex posteriorly, narrow supratympanic stripe, usually diffuse canthal stripe and small, irregular markings on body. Flanks pale creamy-brown with fine dark brown reticulations or diagonal streaks; limbs distinctly barred in nine individuals—two bars on forearm, one or

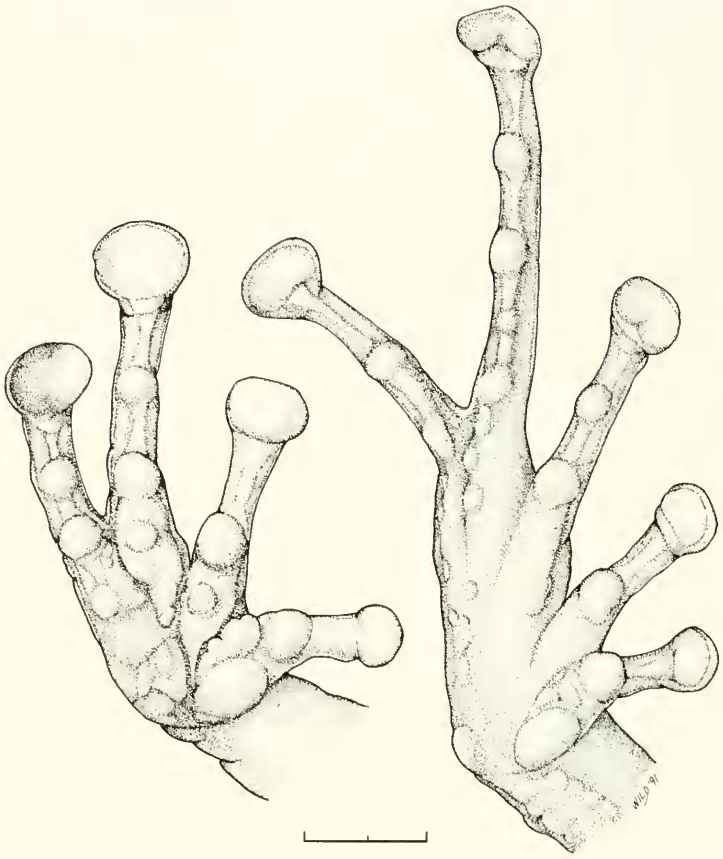

Fig. 9. Hand and foot of holotype of *Eleutherodactylus rhodoplichus*, KU 219786. Scale = 2 mm.

two on thigh, and two or three on shank; posterior surfaces of thighs creamy tan with fine dark brown reticulations; venter cream to tan with numerous brown flecks on throat, belly, and ventral surfaces of thighs. Four males with broad, pale cream dorsolateral stripe extending from supratympanic region to point above cloaca, narrowly bordered by dark brown; narrow cream supracanthal stripes converging on snout; otherwise colored like other individuals. Two males and one female with broad, cream, transverse bar between outer edges of eyelids anterior to interorbital triangle; otherwise colored like other individuals.

Color in life: KU 219786: dorsum reddish tan, flanks tan with black flecks; dorsal surfaces of limbs orange; vocal sac yellow, rest of venter beige (Fig. 8). KU 219791: dorsum dark brown with pale tan dorsolateral stripes; venter dull white with scattered black flecks (Fig. 8). KU 219787: dorsum dark brown with broad, golden-yellow transverse bar between outer edges of eyelids; venter bronze to brown (Fig. 8). In all specimens, inguinal region and anterior and posterior surfaces of thighs rose-red; iris reticulated with gold above, reddish brown below (E. R. Wild field notes, 8 January 1991).

Measurements (in mm; 17 males, followed by four females): SVL 21.8–28.9 (25.8 ± 1.85), 30.1-34.2 (32.5); TL 11.1–13.8 (13.1 ± 0.70), 14.5–16.5 (15.5); FL 10.6–14.3 (12.7 ± 0.94), 14.9–16.1 (15.3); HW 7.1–10.5 (9.5 ± 0.91), 9.6–13.2 (12.0); HL 7.6–10.4 (9.3 ± 0.64), 10.1–12.5 (11.6); IOD 2.7–3.4 (3.0 ± 0.20), 3.3–4.2 (3.8); EW 1.9–2.8 (2.4 ± 0.28), 2.2–3.3 (2.8); E–N 2.1–2.7 (2.4 ± 0.16), 2.2–3.1 (2.8); ED 2.3–3.5 (2.8 ± 0.30), 3.2–3.8 (3.5); TYM 0.9–1.5 (1.2 ± 0.16), 1.1–1.3 (1.2).

Distribution and ecology.—*Eleutherodactylus rhodoplichus* is known from elevations of 2770–3050 m on the western slope to the crest of the Cordillera de Huancabamba in northern Peru. At the crest it inhabits a dense, low forest, whereas lower on the slopes, it inhabits cloud forest; both areas were classified as humid montane forest by Tosi (1960). In late November and early December 1974, Richard Thomas found males calling from low (< 20 cm) herbaceous vegetation at night at the crest of the cordillera. The call is a single, moderately high-pitched note with rising pitch. Males also were calling at the type locality on 8 January 1991. The subadult female from 12.7 km NE of El Tambo was under a rock by day.

Etymology.—The specific name is derived from the Greek *rhodon* meaning rose or red and the Greek *plichas* meaning inside of the thigh. The name refers to the rose-red color on the hidden surfaces of the thighs.

Eleutherodactylus sternothylax new species

Holotype.—KU 219793, an adult male from the western slope of the Cordillera de Huancabamba, 16 km (by road) ENE of Canchaque (05°23'S, 79°34'W, 1840 m), Provincia Huancabamba, Departamento Piura, Peru; one of a series collected on 7 January 1991 by Fernando M. Cuadros, John J. Wiens, and Erik R. Wild.

Paratypes.—KU 219794 and MHNSM 15405–06 collected with the holotype; KU 196479–81, 196483, 196486–89, 196491, LSUMZ 32320, 32332–50, 32352, 32418–27, 32458 from the west slope of the Cordillera de Huancabamba, 15 km (by road) E of Canchaque, 1735 m, Provincia Huancabamba, Departamento Piura, Peru.

Referred specimens.—KU 196482, 196484–85, 196490, juveniles, with same data as KU 196479–81.

Diagnosis.—A member of the *Eleutherodactylus unistrigatus* group characterized by: (1) skin on dorsum shagreened with few, low, round tubercles usually most evident posteriorly and laterally and lacking folds; skin on venter granular; (2) tympanum distinct, round, diameter about half that of eye, situated posterior to eye, separated from eye by distance about one-half diameter of tympanum; (3) snout acuminate in dorsal view, acutely rounded in profile, protruding; canthus rostralis, curved, acutely rounded; (4) upper eyelid narrower than interorbital distance with few, low, round tubercles; cranial crests absent; (5) vomerine odontophores prominent, oval, posteromedially inclined; (6) males with large, median, subgular vocal sac extending posteriorly onto chest; vocal slits present; nuptial excrescences absent; (7) first finger shorter than second; pads large, truncate; pad on Finger III equal to or slightly greater than diameter of tympanum; (8) fingers bearing narrow lateral keels; (9) ulnar surfaces smooth; (10) tubercles absent on heel and tarsus; (11) two metatarsal tubercles; inner large, elliptical, three to four times size of round outer tubercle; few low, diffuse supernumerary plantar tubercles; (12) toes bearing narrow lateral keels, lacking webbing; pads smaller than those on fingers; (13) dorsum tan with dark brown markings consisting of interorbital bar or triangle, labial bars, supratympanic stripe, diagonal bars on flanks, transverse bars on limbs, and variable markings on body—X-, H-, or W-shaped mark in scapular region, one or two chevrons on posterior part of body, longitudinal or diagonal dorsolateral marks, or narrow middorsal line; venter cream with minute brown flecks; (14) adults moderate in size, 39 males 18.3–29.1 mm SVL, six females 28.3–36.7 mm.

Of the members of the *Eleutherodactylus unistrigatus* group in northern Peru and southern Ecuador, nine species are like *E. sternothylax* in having an acuminate snout, distinct and round tympanum, and lacking tubercles on the heel. Five of these (*E. ganonotus, ignicolor, pastazensis, pecki,* and *trachyblepharus*) differ from *E. sternothylax* by having smooth skin on the dorsum; *E. ceuthospilus* differs by lacking visible vomerine odontophores. *Eleutherodactylus proserpens* and *E. wiensi* are smaller than *E. sternothylax;* the former has relatively small, round pads, and the latter has more finely tuberculate skin on the dorsum and lacks diagonal dark marks on the flanks. *Eleutherodactylus phoxocephalus* has more tuberculate skin on the dorsum and lacks diagonal bars on the flanks and transverse bars on the limbs.

Description.—Thirty-nine adult males, six adult females. Head as wide as body, slightly longer than wide; HW 30–39% ($\bar{x}$ = 35 ± 2) of SVL; HL 34–41% ($\bar{x}$ = 37 ± 2) of SVL; snout moderately long, protruding beyond margin of lip; acuminate in dorsal view, acutely rounded in profile; E–N slightly less than ED; E–N 24–32% ($\bar{x}$ = 28 ± 2) of HL; eye moderately large, ED 27–38% ($\bar{x}$ = 31 ± 2) of HL; upper eyelid bearing small, low

tubercles along outer margin, EW 59–96% ($\bar{x} = 81 \pm 9$) of IOD. Top of head flat; cranial crests absent; canthus rostralis slightly curved, acutely rounded; loreal region concave; lip slightly flared anterior to orbit; internarial area barely depressed; nostril ovoid, slightly protruding laterally at point just posterior to anterior margin of lower jaw. Supratympanic fold weak, curving posteroventrally from posterior corner of orbit, barely obscuring dorsal and posterodorsal parts of tympanic annulus; tympanum round, separated from eye by distance less than TYM, which is 36–57% ($\bar{x} = 46 \pm 5$) of ED. Choanae round, widely separated, not obscured by palatal shelf of maxillary arch; vomerine odontophores prominent, elliptical, narrowly separated medially, posteromedially inclined at level behind posterior margins of choanae, each bearing 2–6 ($\bar{x} = 3.5 \pm 1.5$) teeth in males and 4–7 ($\bar{x} = 5.5$) teeth in females. Tongue narrowly elliptical, shallowly notched posteriorly, free behind for about one-fourth of its length; vocal slit elongate, extending from midlateral base of tongue toward angle of jaws; vocal sac large, single, median, beginning near midlength of throat and extending well onto chest (Fig. 10).

Skin on dorsum shagreened (less so in females) with scattered low, round tubercles, most numerous dorsolaterally and posteriorly on body and on dorsal surfaces of thighs; somewhat larger tubercles dorsal and posterior to supratympanic fold; dermal folds absent on dorsum; flanks smooth; skin

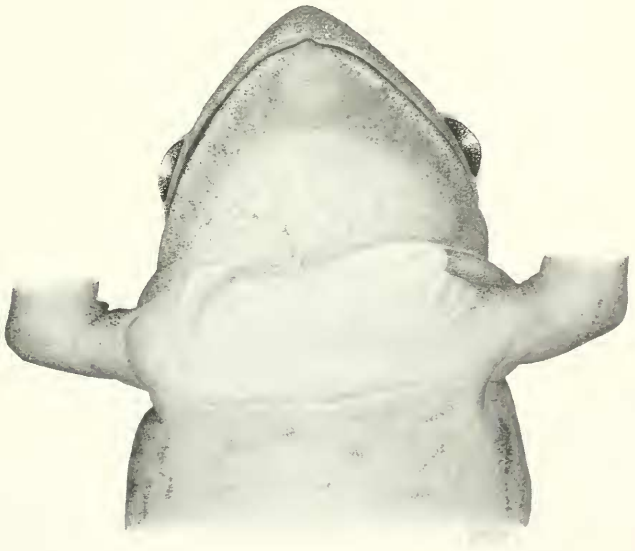

Fig. 10. Adult male of *Eleutherodactylus sternothylax*, KU 196486, showing extent of vocal sac. Scale = 5 mm.

on belly and ventral surfaces of thighs granular; discoidal fold evident; ulnar, tarsal, and heel tubercles absent. Cloacal opening unmodified, directed posteroventrally at upper level of thighs.

Forearm moderately robust; fingers moderately long, slender, bearing narrow lateral keels and broad, truncate discs, widest on Fingers III and IV; relative lengths of fingers I < II < IV < III; subarticular tubercles large, round, elevated; supernumerary tubercles basally on Fingers II–IV; palmar tubercle elevated, distinctly bifid; thenar tubercle elliptical, slightly elevated (Fig. 11); males lacking nuptial excrescences. Hind limb moderately robust, long; heels overlapping slightly when hind limbs flexed at right angles to axis of body; TL 47–59% ($\bar{x}$ = 51 ± 03) of SVL; FL 41–51% ($\bar{x}$ = 46 ± 02) of SVL. Tarsal fold absent; inner metatarsal tubercle large, elliptical; outer metatarsal tubercle small, round; toes long, slender, unwebbed, bearing narrow lateral keels and truncate discs smaller than those on fingers; relative lengths of toes I < II < III < V < IV; subarticular tubercles small, round to subconical; supernumerary tubercles low, round, only on proximal segments of digits (Fig. 11).

Color in preservative: Dorsum of head, body, and limbs tan to grayish tan with dark brown markings consisting of interorbital bar (11 individuals) or triangle with posterior apex (30), connected (13) or not (17) to pattern on dorsum of body consisting of X-, H-, or W-shaped marks in scapular region and diagonal marks or chevrons postscapularly, continuous or not with two or three diagonal marks on flanks (35); middorsum of body unicolor (with narrow dark vertebral line in 4) bordered by dark brown (10), with broad, creamy-tan stripe extending from supratympanic region to groin (4). Limbs distinctly barred (39) with 2 or 3 bars on forearm, 3 or 4 on thighs and shanks, 2 or 3 on tarsi; bars on thighs continuing onto posterior surfaces, separated there by creamy-tan interspaces; posteroventral surfaces of thighs dark brown (34) or creamy tan (11). Narrow dark brown canthal and supratympanic stripes; 1 or 2 narrow, diagonal, suborbital bars. Venter cream with scattered, minute, brown flecks.

Color in life: Dorsum brown to pale greenish tan with contrasting dark brown marks (Fig. 12); pale areas on posterior surfaces of thighs yellow to orange; venter dull white; vocal sac yellow; iris coppery (R. Thomas, field notes, 8 December 1974).

Measurements (in mm; 39 males, followed by 6 females): SVL 18.3–29.1 (24.2 ± 2.39), 28.3–36.7 (32.1); TL 8.7–14.8 (12.3 ± 1.34), 15.1–18.9 (16.8); FL 8.2–14.4 (11.2 ± 1.27), 13.6–17.3 (15.2); HW 6.3–10.6 (8.3 ± 1.06), 10.0–13.0 (11.5); HL 7.1–10.9 (8.9 ± 0.94), 10.4–12.8 (11.5); IOD 2.1–3.3 (2.8 ± 0.27), 3.1–4.0 (3.6); EW 1.6–2.9 (2.3 ± 0.33), 2.1–3.3 (2.6); E–N 1.7–3.3 (2.5 ± 0.33), 2.6–3.6 (3.2); ED 2.0–3.5 (2.8 ± 0.38), 3.2–3.8 (3.5); TYM 0.9–1.6 (1.3 ± 0.17), 1.2–2.0 (1.5).

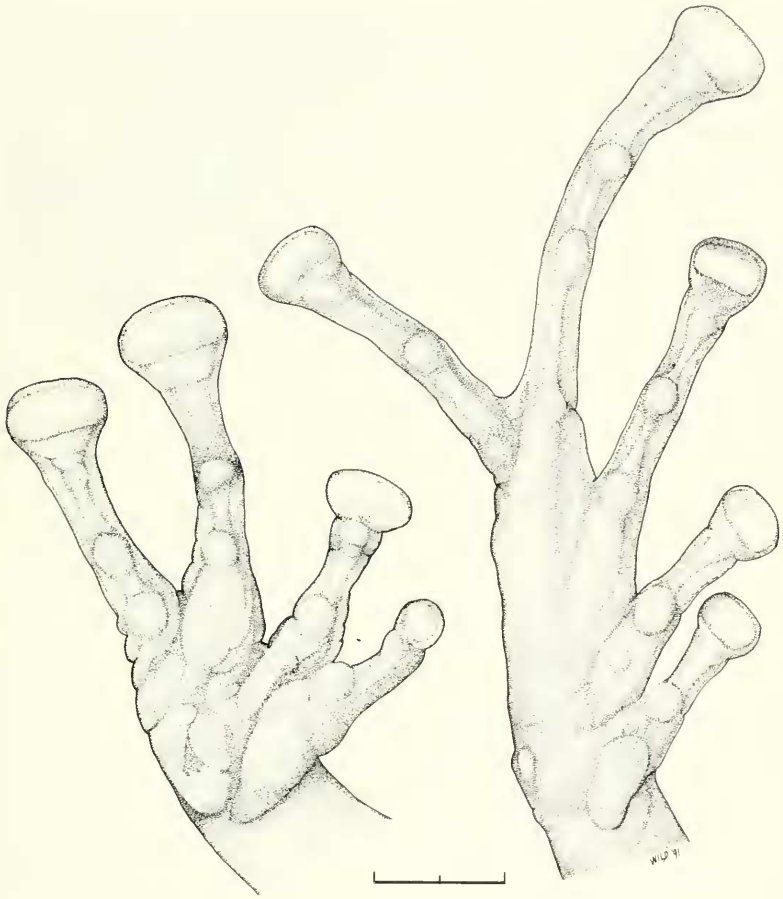

Fig. 11. Hand and foot of holotype of *Eleutherodactylus sternothylax*, KU 219793. Scale = 2 mm.

Distribution and ecology.—This species is known only from elevations of 1735–1840 m on the western slope of the Cordillera de Huancabamba in northern Peru, where it inhabits humid montane forest. In November and December 1974, males were calling from herbaceous vegetation 0.3–1.0 m above the ground. The call is a single "tock" repeated at intervals of about 5 sec. On 7 January 1991, individuals were found on low vegetation in cut-over forest.

Etymology.—The specific name is derived from the Greek *sternon* meaning chest and the Greek *thylax* meaning sack. The name refers to the position of the vocal sac extending onto the chest.

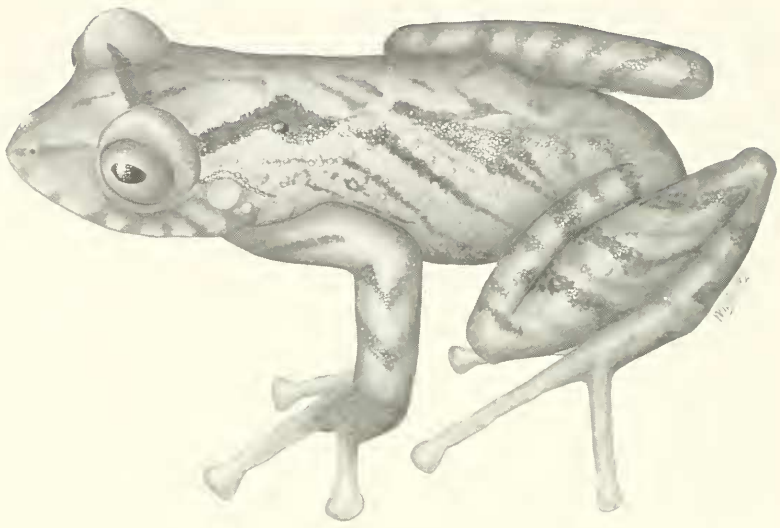

Fig. 12. Holotype of *Eleutherodactylus sternothylax*, KU 219793, adult male, 29.1 mm SVL.

Eleutherodactylus wiensi new species

Holotype.—KU 219795, an adult male, from 12.7 km (by road) ENE of Canchaque (05°24'S, 79°35'W, 1600 m), Provincia Huancabamba, Departamento Piura, Peru; one of a series collected on 7 January 1991 by Fernando M. Cuadros V., John J. Wiens, and Erik R. Wild.

Paratypes.— KU 219796–97 and MHNSM 15407–08 from the type locality; KU 196510–11 from 15 km (by road) ENE of Canchaque, 1735 m, Departamento Piura, Peru.

Diagnosis.—A member of the *Eleutherodactylus unistrigatus* group characterized by: (1) skin of dorsum smooth with scattered, small, conical tubercles, and crescent-shaped fold from orbit into scapular region; skin on venter granular; (2) tympanum barely distinct, round, diameter about one third that of eye, separated from eye by distance slightly less than diameter of tympanum; (3) snout acutely rounded in dorsal view, round in profile, barely protruding; canthus rostralis rounded; (4) upper eyelid narrower than interorbital distance, with tubercles on outer margin or not; cranial crests absent; (5) vomerine odontophores prominent; (6) males with large, median, subgular vocal sac; vocal slits present; nuptial excrescences absent; (7) first finger shorter than second; pads large, truncate; width of pad on Finger III 1.5 times diameter of tympanum; (8) fingers with narrow lateral keels; (9) few low, diffuse ulnar tubercles; (10) single subconical tubercle on heel; outer edge of tarsus with few low, round tubercles; tarsal fold low,

present distally; (11) two metatarsal tubercles; inner large, ovoid, four times size of subconical outer tubercle; many low, minute supernumerary plantar tubercles; (12) toes with lateral keels, and basal webbing; pads on Toes III and IV equal to, or slightly smaller than, those on fingers; (13) dorsum grayish tan with irregular brown markings; flanks cream with dark brown mottling; dark brown canthal and supratympanic stripe and interorbital and labial bars; posterior surfaces of thighs brown with cream spots; venter cream with brown spots or reticulation; (14) adults medium-sized, six males 27.8–33.0 mm SVL, one female 37.0 mm SVL.

Among the species in the *Eleutherodactylus unistrigatus* group in Peru and southern Ecuador, *E. wiensi* superficially resembles *E. cajamarcensis*, *E. petrobardus*, and *E. versicolor*. However, all three of these species lack dorsolateral folds (weak folds in *E. wiensi*). *Eleutherodactylus cajamarcensis* differs further from *E. wiensi* by having rows of pustules on the dorsum and only moderate-sized, elliptical pads. *Eleutherodactylus petrobardus* differs by having elliptical, instead of truncate discs, and by lacking spots on the venter. *Eleutherodactylus versicolor* differs from *E. wiensi* by lacking vocal slits and by having elliptical pads, many distinct spots on the dorsum, and dark reticulations on the venter.

Description.—Six adult males, one adult female. Head as wide as body, as long as wide; HW 36–39% ($\bar{x}$ = 38) of SVL; HL 37–39% ($\bar{x}$ = 38) of SVL; snout moderately long, slightly protruding beyond margin of lip; acutely round in dorsal view, round in profile; E–N slightly less than ED; E–N 24–31% ($\bar{x}$ = 27) of HL; eye moderately large, ED 27–32% ($\bar{x}$ = 30) of HL; upper eyelid smooth or with few low tubercles on outer margin, EW 68–96% ($\bar{x}$ = 82) of IOD. Top of head flat; cranial crests absent; canthus rostralis slightly curved, rounded; loreal region barely concave; lip not flared anterior to orbit; internarial area slightly depressed; nostril round, distinctly protruding laterally at point above anterior margin of lower jaw. Supratympanic fold moderately weak, curving posteroventrally from posterior corner of orbit, obscuring dorsal and posterodorsal parts of indistinct tympanic annulus; tympanum round, separated from eye by distance slightly less than TYM, which is 32–41% ($\bar{x}$ = 37) of ED. Choanae small, ovoid, widely separated, not obscured by palatal shelf of maxillary arch; vomerine odontophores prominent, widely separated medially, slightly posteromedially inclined far posterior to level of choanae, each bearing three or four ($\bar{x}$ = 3.7) teeth. Tongue broadly elliptical, shallowly notched posteriorly, free behind for about one-fourth of its length; vocal slit elongate, extending from midlateral base of tongue toward angle of jaws; vocal sac large, single, median, subgular.

Skin on dorsum of head, body, and limbs, and on flanks smooth with scattered, small, conical tubercles; low, tuberculate, crescent-shaped dermal folds extending from posteromedial border of upper eyelid to posterior part

of scapular region; belly and posteroventral surfaces of thighs granular; other ventral surfaces smooth; discoidal fold evident; two or three diffuse ulnar tubercles distally; heel with single subconical tubercle; one to three low, diffuse tubercles on outer edge of tarsus. Cloacal opening unmodified, directed posteroventrally at upper level of thighs, bordered below by numerous tubercles.

Forearm moderately slender; fingers long, slender, bearing narrow, lateral keels and broad, truncate discs; disc on Finger I noticeably smaller than those on other fingers; relative lengths of fingers I < II < IV < III; subarticular tubercles large, round; few supernumerary tubercles basally on Fingers III–IV; palmar tubercle elevated, distinctly bifid; thenar tubercle large, elliptical, elevated (Fig. 13); males lacking nuptial excrescences. Hind limbs moderately robust; heels broadly overlapping when hind limbs flexed at right angles to axis of body; TL 52–59% ($\bar{x}$ = 56) of SVL; FL 50–54% ($\bar{x}$ = 52) of SVL. Low inner tarsal fold on distal half of tarsus; inner metatarsal tubercle large, ovoid; outer metatarsal tubercle small, subconical; toes long, slender, unwebbed, bearing narrow lateral keels and truncate discs slightly smaller than those on fingers; relative lengths of toes I < II < III < V < IV; subarticular tubercles small, round; supernumerary tubercles diffuse, only on proximal segments of digits (Fig. 13).

Color in preservative: Dorsum of head, body, and limbs gray to pale brown, with dark brown markings consisting of interorbital bar; median dark mark on occiput; usually three or four irregular spots medially between occiput and posterior end of body (absent in two specimens); broad dorsolateral mark extending from posterior edge of eyelid to groin (3) or irregular markings dorsolaterally. Dark brown canthal and supratympanic stripes; 3 dark brown diagonal suborbital bars; limbs marked by transverse to diagonal bars—2 on forearm, 3 or 4 on thigh and shank, 2 or 3 on tarsus; distinct bars also present on digits; flanks cream with dark brown mottling. Posterior surfaces of thighs brown with numerous small, cream spots (only distally in 3 specimens). Venter creamy white with small, irregular dark brown spots, most numerous on throat and chest in males; few brown flecks on throat and chest of female.

Color in life: Dorsum green (tan middorsally in 1 specimen) with scattered bronze and dark brown blotches (Fig. 14); venter yellow to white; vocal sac yellow with gray flecks; inguinal region with reddish hue in one specimen; iris bronze above, reddish brown below (E. R. Wild field notes, 7 January 1991).

Measurements (in mm; 6 males, followed by 1 female): SVL 27.8–33.0 (30.7), 37.0; TL 16.1–17.4 (16.9), 21.6; FL 14.9–16.8 (15.9), 19.2; HW 10.2–12.8 (11.6), 14.3; HL 10.7–12.5 (11.7), 13.8; IOD 2.7–4.1 (3.4), 4.1;

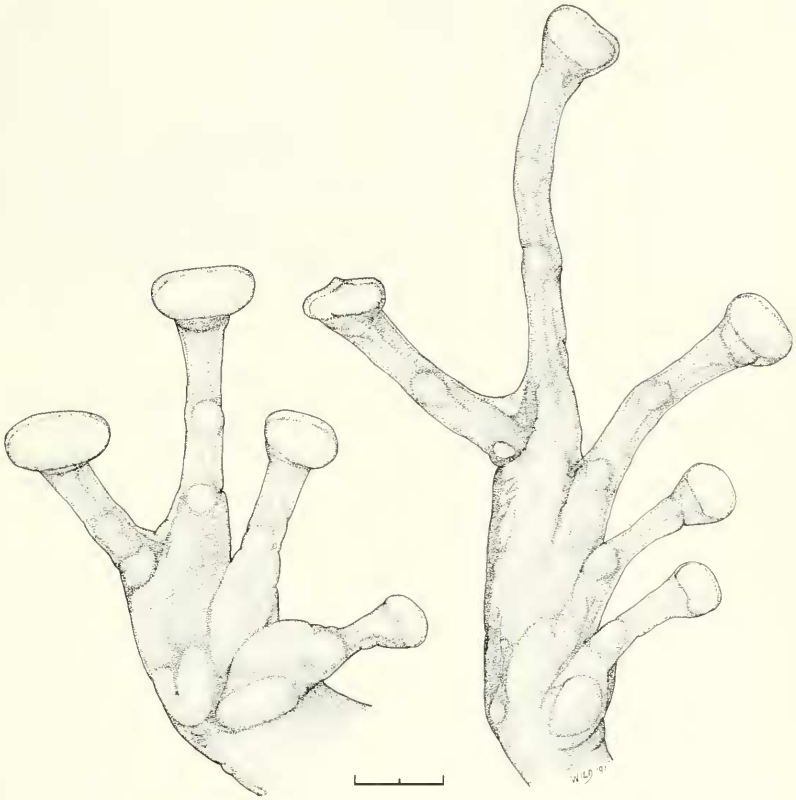

Fig. 13. Hand and foot of holotype of *Eleutherodactylus wiensi*, KU 219795. Scale = 2 mm.

EW 2.1–3.3 (2.8), 3.0; E–N 2.7–3.8 (3.1), 4.1; ED 2.9–4.0 (3.5), 4.2; TYM 1.1–1.4 (1.3), 1.6.

Distribution and Ecology.—*Eleutherodactylus wiensi* is known from only two localities at elevations of 1600 and 1735 m in humid montane forest on the western slope of the Cordillera de Huancabamba in northern Peru. In January 1991, males were calling from low vegetation in cut over cloud forest at night.

Etymology.—The specific name is a patronym for John J. Wiens in recognition of his intense efforts in sampling the herpetofauna of the Andes in northern Peru.

Fig. 14. **Left:** Holotype of *Eleutherodactylus wiensi*, KU 219795, adult male, 32.1 mm SVL. **Right:** *Eleutherodactylus* sp., KU 219798, male, 20.4 mm SVL.

ACCOUNTS OF NAMED TAXA

Centrolenidae

Centrolene buckleyi (Boulenger, 1882)

Two metamorphosing young (KU 181884) from 3010 m on the eastern slope of the cordillera are the first specimens of this species recorded from Peru. The SVLs are 17.3 and 18.6 mm, and the tail stubs are 4.3 and 10.8 mm, respectively. In life, the dorsum was bright green with white labial, lateral, and tarsal stripes; the throat was green, and the venter was transparent. The iris was yellowish bronze. In preservative, the dorsum is pale lavender, and the venter is white. The first and second fingers are equal in length. The webbing formula for the outer fingers is III 3—2⁺ IV and for the toes, I 1—2 II 1½—2) —2 III 1½—2⁻ IV 2 —2 V. The humeral spine is not evident externally. These small specimens compare favorably with metamorphosing young (KU 170221) from 14.5 km WSW of Leticia, 2540 m, Departamento Cauca, Colombia. One individual was under a rock and the other in bunchgrass, both at the edge of a small stream by day on 26 February 1979. We follow Ruíz-Carranza and Lynch (1991) in assigning centrolenids having a humeral spine to the genus *Centrolene*.

Dendrobatidae

Colostethus elachyhistus Edwards, 1971

This species is common along streams at lower elevations along the transect; 53 specimens are from: Canchaque, 1120 m, KU 137923–24, 138811–12, KU 219750–52, MHNSM 15379–81; 8.5 km W Canchaque, 620 m, KU 219745–49, MHNSM 15374–78; 12 km E Canchaque, 1770 m,

KU 181643; Huancabamba, 1840 m, KU 138062–70, 181644–66. These are the only Peruvian localities for the species. In the vicinity of Canchaque, the frogs were in a rocky stream bed in tropical dry forest; at Huancabamba, they were around a swampy pool in a riverbed and in a small pool in a small patch of dry forest surrounded by cultivated fields.

In life, specimens from Huancabamba had a brown dorsum with dark brown or black markings; the flanks were dull brown, and the lateral stripe was dull creamy tan. The belly was pale creamy yellow with gray mottling, and the throat was creamy white with a gray suffusion; the iris was grayish brown. In contrast, the specimens from the vicinity of Canchaque had a yellowish-olive dorsum with black blotches, a silvery white lateral stripe, a white venter, and a reddish-brown iris (Fig. 15).

Comparison of these specimens with the holotype (KU 120540) and other specimens (KU 120515–39, 120541, 138800–10, 142344–76, 166091–93) of *Colostethus elachyhistus* from the Loja Basin in Ecuador reveals that the specimens from Huancabamba are most like the typical material, but have slightly more webbing between the outer toes, whereas the specimens from the vicinity of Canchaque have considerably more webbing between the outer toes and a more pallid venter. In preservative, typical *C. elachyhistus* have faint pale spots on the chest and belly; these spots are evident in the specimens from Huancabamba and are faint or absent in those from Canchaque. The only other species like *C. elachyhistus* in structure and coloration is *C. infraguttatus* (Boulenger, 1898) from the lower Pacific slopes of the Andes in Ecuador. This species lacks webbing between the outer toes and has more distinctive spots on the venter. Comparison of the Peruvian specimens with series of *C. infraguttatus* from Provincia El Oro, Ecuador, reveals that the Peruvian specimens are more like *C. elachyhistus* than *C. infraguttatus*.

Fig. 15. **Left:** *Colostethus elachyhistus*, KU 219745, female, 20.4 mm SVL. **Right:** *Colostethus sylvaticus*, KU 138071, female, 23.9 mm SVL.

Tadpoles were described and illustrated by Edwards (1971). Tadpoles (KU 181867) were found in a small pool at Huancabamba on 27 February 1979, (KU 219754) in a muddy pool 8.5 km west of Canchaque on 7 January 1991, and (KU 219753, MHNSM 15382) in quiet parts of a stream at Canchaque on 7 January 1991. In life, those from Huancabamba had a dull brown body and a cream tail with a reddish-brown midlateral line proximally; the fins were translucent with gray flecks. In life, those from Canchaque had a dark gray to olive body and the tail yellow proximally becoming more orange posteriorly; the entire tail was flecked with gray.

The slight differences in webbing and coloration in adults and coloration of tadpoles among samples from Canchaque, Huancabamba, and the Loja Basin suggest the possibility that more than one species is included in this nominal taxon. More specific assignments of these populations necessitates a thorough review of the *Colostethus* of the semiarid basins and valleys in northern Peru and southern Ecuador, where we are aware of two unnamed taxa—one at Abra de Porculla, Departamento Piura, and one in the Marañón Valley, Departamento Amazonas, Peru.

Colostethus sylvaticus (Barbour and Noble, 1920)

This large *Colostethus* was found only at higher elevations in the cordillera; 22 specimens (KU 138071–79, 181667–79) are from elevations of 3010–3100 m on the eastern slope; KU 219755 from 1 km W of El Tambo and KU 219156–58 and MHNSM 15383–86 from 12.7 km E of El Tambo are from elevations of 2770–2820 on the western slope. All individuals were active in, or under rocks along, small streams in cloud forest.

In life, the dorsum was olive-brown to coppery brown with dark brown or black flecks. The labial and lateral stripes were pale bronze to creamy tan. The throat, posterior part of the belly, and ventral surfaces of the hind limbs were dark yellow to orange; the chest and anterior part of the was pale gray with black flecks. The iris was dull bronze, heavily flecked with black (Fig. 15).

Comparison of these specimens with the holotype (MCZ 5344) and four paratopotypes (MCZ 5346, 5350, 5355–56) reveals no differences in structure. The color pattern of the types is faded, and there is no evidence of pigmentation ventrally.

A male (KU 181673) having a SVL of 25.7 mm was carrying 15 tadpoles (KU 181868), 12.1–13.2 ($\bar{x}$ = 12.8, n = 9) mm in total length. Free-swimming tadpoles (KU 181869–70) were obtained from muddy pools at 3010 and 2560 m on the eastern slope. Mean total length at Stage 33, 29.7 ± 1.63 mm (27.8–31.7 mm, n = 10); body length 42% of total length, 1.6 times longer than wide; 2.1 times longer than high; 1.3 times wider than high (Fig. 16); body in dorsal view elongately ovoid, widest just

posterior to level of eyes; body in lateral view compressed, highest posteriorly; eyes dorsal, directed dorsolaterally; interorbital distance approximately twice diameter of eye; snout in dorsal view subacuminate, in lateral view rounded; nares small, dorsal, directed laterally, about one-half distance from anterior edge of eye to tip of snout; internarial distance approximately equal to eye diameter, spiracle sinistral, below midline, spiracular tube not free, opening directed posteriorly at point about two-thirds length of body; vent tube medial at body, attached dextrally to ventral fin for entire length. Caudal musculature highest at tail-body junction, not narrowing until about midlength, gradually narrowing posteriorly, terminating short of tail tip; in lateral view, dorsal fin terminating at dorsal tail-body junction, highest at about two thirds length of tail; height equal to, or greater than, musculature at midlength; ventral fin higher than dorsal fin anteriorly, same height posteriorly; height equal to, or greater than, musculature at midlength; greatest height of tail at about midlength.

Oral disc anteroventral and not emarginate (Fig. 16); one row of moderately large, distinct marginal papillae with moderate-sized medial gap on upper labium; second row of marginal papillae present laterally on lower labium in some specimens (KU 181870); submarginal papillae rarely present laterally near ends of labial tooth rows; LTRF 2/3(1); jaw sheaths moderately robust, finely serrate; upper sheath narrow, widely arched; lower sheath widely V-shaped.

In preservative, posterior half of body dark brown, with unpigmented transverse bands ventrally in some specimens. Dorsum of anterior half of body pale brown with dark brown blotch between eyes; anterior part of venter unpigmented. Caudal fins transparent with pale brown pigmentation, especially on dorsal fin; brown lateral stripe at midheight on anterior one fourth of tail. In life, the body and tail olive-tan with green lichenous markings dorsally on caudal musculature; belly greenish white; border of oral disc yellow; iris pale bronze.

The type locality was given by Barbour and Noble (1920:396) as "Tabacónas (near Huancabamba) northwestern Peru." Tabacónas is at an elevation of 1892 m in the valley of the Río Tabacónas, which is on the east side of a north-south ridge more than 3000 m above sea level; Huancabamba is at an elevation of 1840 m in a broad valley to the west of this ridge. According to the catalogue in the Museum of Comparative Zoology, the locality is "Tabacónas, cordilleras, 10 mi. W of Tabamas, 8000 ft." This elevation, 2469 m, approximates the lowest elevations for the species on the western slope of the Cordillera de Huancabamba. Apparently *C. sylvaticus* is restricted to elevations above 2400 m on two adjacent ridges separated by the valley of the Río Huancabamba.

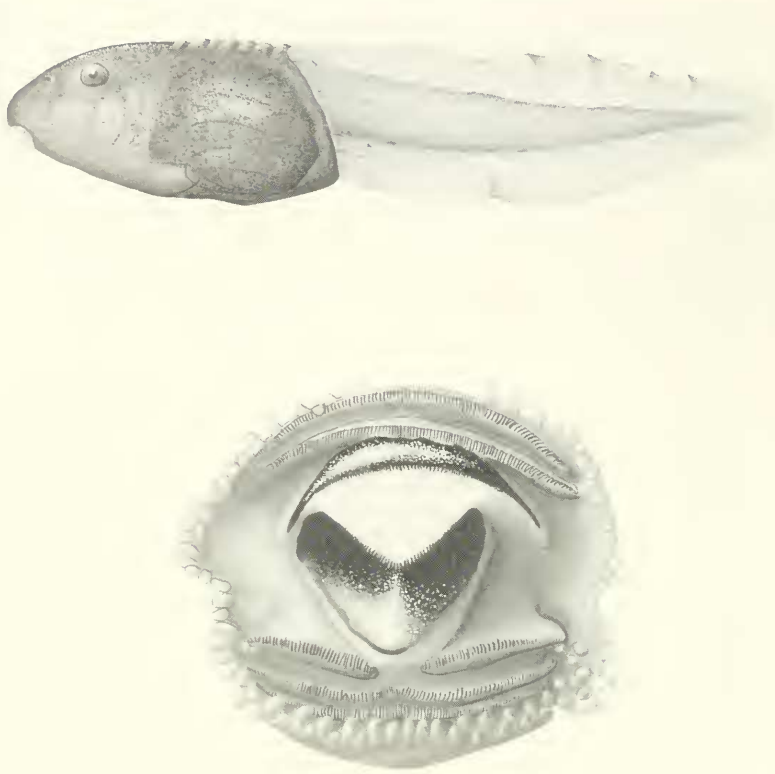

Fig. 16. Tadpole (top, scale = 5 mm) and external oral features (bottom, scale = 1 mm) of *Colostethus sylvaticus*, Stage 33, KU 181869.

Epipedobates tricolor (Boulenger, 1899)

Specimens from Canchaque, 1120 m (KU 219762–64, MHNSM 15413–15) and 8.5 km W Canchaque, 620 m (KU 219759-61, MHNSM 15409–12) were found in leaf litter near a stream in dry tropical forest on 7 January 1991. In life, the dorsum was pale green with black dorsolateral stripes (Fig. 17); the venter was white heavily mottled with dark brown or black, and the spots on the hind limbs were bright red.

Based on the descriptions and comparisons made by Silverstone (1976) and series of specimens (KU 142532–602, 152083–145, 166161–62) from localities as low as 20 m at 11.5 km SE of Machala, Provincia El Oro, to 1690 m at 17 km SW of Girón, Provincia, Azuay, Ecuador (Fig. 19), we find no morphological characters by which to distinguish *Epipedobates anthonyi* from *E. tricolor*. Rivero (1991) was puzzled that a specimen

Fig. 17. *Epipedobates tricolor:* **Left:** KU 219760, female, 18.8 mm SVL, from 8.5 km W of Canchaque, Departamento Piura, Peru. **Right:** KU 142590, male, 18.8 mm SVL, from 12.6 km W Piñas, Provincia El Oro, Ecuador.

(MCZ A103924) that he designated as the holotype of *Colostethus paradoxus* did not fit into any of his phenetic groups of *Colostethus*. From Rivero's description, it is obvious that he based his new species on a specimen of *E. tricolor;* this was confirmed by examining the holotype. Thus, we place *Phyllobates anthonyi* Noble, 1921, and *Colostethus paradoxus* Rivero, 1991, as junior synonyms of *Prostherapis tricolor* Boulenger, 1899.

The records from the vicinity of Canchaque are the southernmost localities for this species, which has an altitudinal range from sea level to 1770 m and a geographic range from southeastern Provincia Bolívar and western Provincia Azuay, Ecuador, southward to Canchaque, Peru. Other documented records from Peru are Huasimal, Departamento Piura, and Pozo Azul, Departamento Túmbes (Silverstone, 1976).

Hylidae

Gastrotheca galeata Trueb and Duellman, 1978

This casque-headed marsupial frog is known only from intermediate elevations (1740–2130 m) on the western slopes of the cordillera. It is represented in the collections by 16 specimens (KU 174361–65, 181700, KU 219765, 219766, LSUMZ 32050–53, 32058–59, MHNSM 15417, 15416). All are adults except KU 219766, a juvenile with a SVL of 15.6 mm that differs from adults by having intense reddish-orange toe discs and ventral surfaces of the limbs. Some individuals were found in crevices between rotten logs and soil and beneath stones in a scrubby pasture by day. At night, one was on a mossy bank and four were on bushes and trees to a height of about 4 m.

Gastrotheca lateonota Duellman and Trueb, 1988

This species is known only from 13 adult females (KU 181729–38, 181836–37, MHNSM 1635) from El Tambo, 2770 m, on the western slope of the cordillera. All were found on the night of 17 February 1979 as they were moving into a depression filling with water after a heavy rain.

Gastrotheca monticola Barbour and Noble, 1920

We obtained nine specimens (KU 219767–71, MHNSM 15418–21) from Huancabamba, the type locality of the species, and its environs in January 1991. All were found at night. One was perched on a leaf of a plant in town, and the others were on bushes in arid cultivated areas.

Leptodactylidae

Eleutherodactylus cajamarcensis Barbour and Noble, 1920

Individuals (KU 135495, 135502, 181244–61, 196508) of this small species were found under logs and rocks and in arboreal bromeliads by day on the crest and the higher eastern slopes of the cordillera at elevations of 3050–3100 m. In life, the dorsum was yellowish tan, reddish brown, or dark brown, with or without a cream interorbital bar and tan dorsolateral stripes; the venter was cream with dark gray flecks, and the iris was bronze with a median horizontal red streak. These specimens agree well with specimens reported from southern Ecuador by Lynch (1969; 1979).

Eleutherodactylus colodactylus Lynch, 1979

This species is represented by 29 specimens (KU 135494, 135496–501, 181262–64, 196443–61) from the crest and upper eastern slopes of the cordillera (2745–3110 m). All individuals were found in small terrestrial and arboreal bromeliads by day. In life, the dorsum was yellowish tan, pinkish tan, or pale red with dark brown markings; the venter was creamy gray, and the iris was reddish bronze. In structure and color pattern these specimens are like the type series from Abra de Zamora, Provincia Loja, Ecuador, except that the Peruvian specimens are slightly larger—SVL in males 16.8–19.6 mm ($\bar{x} = 18.3 \pm 0.4$, $n = 19$) vs 15.6–18.2 mm ($\bar{x} = 17.0 \pm 0.6$, $n = 8$); females 19.1–23.2 mm ($\bar{x} = 21.5 \pm 0.9$, $n = 9$) vs 20.2–21.2 mm ($\bar{x} = 20.6 \pm 0.3$, $n = 6$) (Lynch, 1979). The species is known in Peru only from the Cordillera de Huancabamba.

Eleutherodactylus cryptomelas Lynch, 1979

Two juvenile females (KU 181269 and MHNSM 15398) from the vicinity of El Tambo at 2770–2820 m on the western slope of the cordillera

represent the first records for this species from Peru. One was under a rock by day and the other in a tree at night. These specimens are 22.0 and 18.2 mm SVL. In life, KU 181269 had a tan dorsum with dark brown markings; the venter was cream with dark brown spots, and the iris was pale bronze with a median horizontal red streak. These specimens are like the type series in structure, but both have less black in the groin and on the posterior surfaces of the thighs and they have more numerous dark flecks on the venter.

Eleutherodactylus lymani Barbour and Noble, 1920

This large, terrestrial species is represented by a single specimen (MHNSM 11172) from Canchaque, 1120 m and eight specimens (KU 196465–69, 181265–67) from 15 km E of Canchaque, 1850 m. The former locality is in dry tropical forest, and at the latter locality, one individual was under a rock by day and the others on the ground at night in humid montane forest. This species has been recorded from several localities in southern Ecuador and northern Peru, including Palambla near Huancabamba, by Barbour and Noble (1920), Lynch (1969), and Duellman (1992) who provided a distribution map.

Eleutherodactylus phoxocephalus Lynch, 1979

Two specimens (KU 181271 from 15 km ENE of Canchaque, 1850 m; MHNSM 15399 from El Tambo, 2770 m) from the western slope of the Cordillera represent the first records for this species from Peru. The first specimen was on a mossy cliff at night; it is a male with a SVL of 26.6 mm and agrees well with specimens from Provincia Loja, Ecuador (Lynch, 1979). In life, the dorsum was brown with black markings and yellow flecks; the venter was dusty cream with a yellow vocal sac, and the iris was dull bronze with a median horizontal red streak. The second specimen was calling from low vegetation at night. It is small for a calling male (SVL 22.7 mm) and differs slightly from specimens from Provincia Loja, Ecuador, by having a somewhat more tuberculate dorsum and only minute dark flecks on the venter.

Eleutherodactylus species

One specimen (KU 219798) cannot be associated with any named species. The diagnostic characters are: (1) Skin on dorsum finely tuberculate, lacking dermal folds; larger tubercles below tympanum and on edge of posterior part of upper jaw; venter coarsely granular; (2) tympanum round, distinct, situated posterior to eye and separated from eye by distance slightly less than diameter of tympanum; (3) snout short, acuminate in dorsal view, truncate and posteriorly inclined in profile; tubercle on tip of

snout; (4) interorbital area flat, greater than width of eyelid; cranial crests absent; (5) vomerine odontophores absent; (6) vocal slits present; vocal sac single, median, subgular; (7) first finger shorter than second; toe discs moderately small, subtruncate; (8) fingers bearing narrow lateral keels; (9) a row of low, diffuse ulnar tubercles; (10) tubercles absent on heel; row of low tarsal tubercles; (11) inner metatarsal tubercle broadly ovoid, about 5 times size of subconical outer metatarsal tubercle; (12) toes unwebbed, bearing narrow lateral keels (13) in preservative, dorsum uniform yellowish tan; venter creamy white with minute black flecks; (14) measurements of one male: SVL 20.4, TL 10.7, FL 9.9, HW 7.5, HL 7.2, IOD 2.6, EW 2.0, ED 2.0, TYM 1.1.

In life, the dorsum of the head, body, and limbs were orange-red (Fig. 14); the flanks, ventral surfaces of the limbs, upper lips, loreal region, tympanum, and vocal sac were yellow. The rest of the venter was cream. The tubercles on the dorsum, flanks, and venter were white, and the iris was bronze with black reticulations and a reddish horizontal streak. The frog was calling from a red leaf 0.5 m above the ground at El Tambo (2770 m) at 20:00 hr on 8 January 1991.

Phrynopus nebulanastes Cannatella, 1984

In addition to the type series listed by Cannatella (1984), we have 23 additional specimens (KU 219806–17, MHNSM 15435–44, 15449) from El Tambo, 2770 m, and four from above El Tambo at an elevation of 2820 m (KU 219818–19, MHNSM 15447–48). All were found under rocks in humid montane forest.

Phrynopus parkeri Lynch, 1975

In addition to the specimens listed by Lynch (1975), we have several large series of specimens (KU 181288–356, 181393, 196581–91, 219820, MHNSM 15445–46, 15450) from El Tambo at 2770 m on the western slope, the summit of the cordillera, and down to 2940 on the eastern slope of the cordillera. All were under rocks in humid montane forest or in the bunchgrass-*Baccharis* association on the summit.

Phyllonastes heyeri Lynch, 1986

In addition to two specimens from Alamor, Provincia Loja, Ecuador, this minute frog is known only from seven specimens collected in the Cordillera de Huancabamba by Richard Thomas in November and December 1974. Lynch (1986) listed all of these specimens as being from 33 km SW of Huancabamba, but according to the LSUMZ catalogue, one specimen (LSUMZ 32134) is from 15 km E of Canchaque, 1760 m. However, David C. Cannatella (pers. comm.) indicated that this may be an

error. Consequently, until this species is confirmed to occur at lower elevations, its distribution in the Cordillera de Huancabamba is considered to be restricted to the summit.

Telmatobius ignavus Barbour and Noble, 1920

This aquatic frog was found in a spring-fed pool at El Tambo, 2770 m (KU 181440–43, 219821) and 29 km E of Canchaque, 3000 m (FSM 34089), on the western slope, and under rocks along streams at elevations of 2820–3010 m on the eastern slope of the cordillera (KU 181438–39, 219822, MHNSM 15466–67). Tadpoles (KU 181846–47, 219823, MHNSM 15468) were found in rocky streams at elevations of 2320, 2820, and 3080 m on the eastern slope and at 2770 m on the western slope (KU 181845). The adults and tadpoles were described by Wiens (1992).

ALTITUDINAL AND ECOLOGICAL DISTRIBUTION

Altitudinal Distribution and Habitat

Of the 21 species in the anuran fauna of the Cordillera de Huancabamba, 17 occur on the western slope between 620 m and the summit at 3110 m (Fig. 18). Eight species occur on the eastern slope between the city of Huancabamba at 1840 m and the summit. Four species occur on both slopes; of these, *Colostethus sylvaticus*, *Phrynopus parkeri*, and *Telmatobius ignavus* are found only at high elevations (2320–3100 m), whereas *Colostethus elachyhistus* does not occur above 1850 m on either slope. Few species have wide altitudinal ranges. Some species (e.g., *Gastrotheca lateonota*) have been found at only a single locality and most species are known from a narrow range of altitudes.

The Cordillera de Huancabamba possesses four general habitats defined by elevation, vegetation, and moisture. These habitats and their anuran constituents are as follow.

Western slope: Below 1700 m ; tropical dry forest, much of which has been cleared for agriculture and pasture: *Colostethus elachyhistus*, *Eleutherodactylus lymani*, *E. wiensi*, and *Epipedobates tricolor*. Elevations of 1700–3000 m; humid montane forest: *Eleutherodactylus ceuthospilus*, *E. cryptomelas*, *E. phoxocephalus*, *E. rhodoplichus*, *E. sternothylax*, *E.* sp., *Gastrotheca galeata*, *G. lateonota*, *Phyllonastes heyeri*, and *Phrynopus nebulanastes*.

Summit: Elevations of 3000–3110 m; humid montane forest characterized by dwarfed trees, a great amount of moss, dense bunchgrass-*Baccharis* association, and numerous arboreal and terrestrial bromeliads; this area is frequently bathed in fog and receives much more rain than the lower slopes: *Centrolene buckleyi*, *Colostethus sylvaticus*,

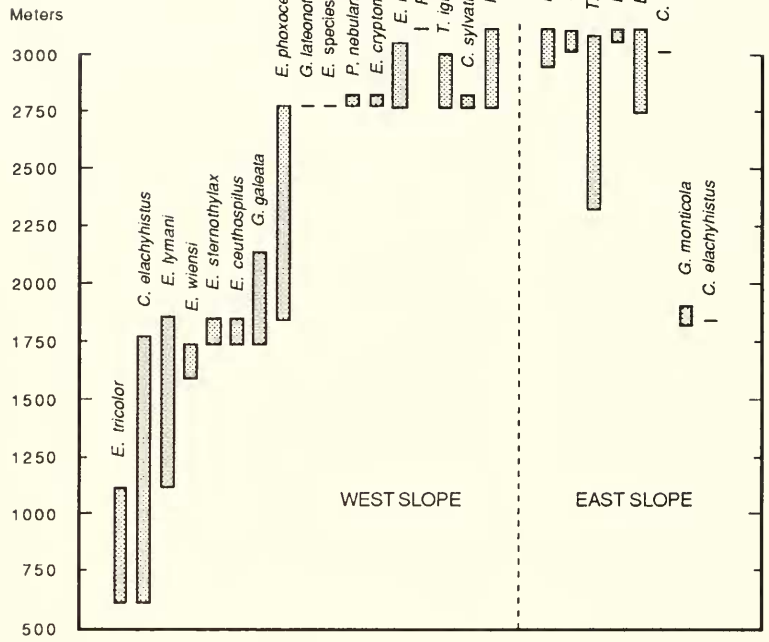

Fig. 18. Altitudinal distribution of anurans in the Cordillera de Huancabamba.

Eleutherodactylus cajamarcensis, *E. colodactylus*, *Phrynopus parkeri*, and *Telmatobius ignavus*.

Eastern slope: Elevations of 1840–3000 m; tropical dry forest, extensively cultivated, much drier than western slope: *Gastrotheca monticola* and *Colostethus elachyhistus*.

The upper and lower extremes (1700–3000 m) of the humid montane forest on the western slope have different assemblages of species. At the lower extreme (1700–2000 m) are *Eleutherodactylus sternothylax*, *E. ceuthospilus*, and *Gastrotheca galeata*. In addition, three of the species predominantly inhabiting tropical dry forest at lower elevations have been found above 1700 m—*Colostethus elachyhistus* to 1770 m, *Eleutherodactylus lymani* to 1850 m, and *E. wiensi* to 1735 m. *Epipedobates tricolor* has been found only in tropical dry forest below 1120 m. Toward

the upper extreme of the humid montane forest, at elevations (< 3000 m) below the level where trees are dwarfed and mosses and bromeliads are abundant. *Eleutherodactylus cryptomelas*, *E. rhodoplichus*, *E.* sp., *Gastrotheca lateonota*, and *Phrynopus nebulanastes*, are found. In addition, three species that presumably occur over the summit, have been found below 3000 m—*Colostethus sylvaticus*, *Phrynopus parkeri*, and *Telmatobius ignavus* down to 2770 m. Of the species restricted to the western slope, only *Eleutherodactylus rhodoplichus* and *Phyllonastes heyeri* occur above 3000 m. Only *Eleutherodactylus phoxocephalus* and *Phyllonastes heyeri* occur at the lower and upper extremes of the humid montane forest. *Phrynopus parkeri* and *Telmatobius ignavus* are found above 3000 m, and *Colostethus sylvaticus* above 2800 m, on both slopes; these species presumably occur over the summit. On the eastern slope, three additional species (*Eleutherodactylus cajamarcensis*, *E. colodactylus*, and *Centrolene buckleyi*) are found above 3000 m. Of the species at high elevations on the eastern slope, only *Telmatobius ignavus* and *Eleutherodactylus colodactylus* are found as low as 2750 m. *Colostethus elachyhistus* and *Gastrotheca monticola* are the only species at low elevations (< 2000 m) in tropical dry forest on the eastern slope.

Altitudinal distributions seem to be closely correlated with habitat. On the western slope there is a distinct change in the anuran fauna where the tropical dry forest gives way to the humid montane forest. The large number of species of anurans in the extensive humid montane forest (1700–3000 m) on the western slope probably is a result of high humidity and habitat heterogeneity. Few species occur throughout the elevational range of this forest; instead, altitudinal replacement of species is evident (Fig. 18). Similar patterns of altitudinal parapatry were noted for anurans on the Amazonian slopes of the Andes in Ecuador by Duellman (1979) and Lynch and Duellman (1980).

Differences in the anuran assemblage in the humid montane forest (1700–3000 m) and that in the dwarfed forest above 3000 m are less distinct. Most species that occupy the summit also occur in the upper extreme of the montane forest, and other species characteristic of the upper montane forest nearly reach the summit. Essentially there is a diminution of species with increasing elevation above about 2800 m.

There are far fewer species on the eastern slope; most of these occur above 3000 m where the ridge is moist and bathed in fog. Only the aquatic *Telmatobius ignavus* has a broad elevational range (2320–3010 m) on the eastern slope. At lower elevations on the eastern slope in the tropical dry forest are *Gastrotheca monticola* and *Colostethus elachyhistus*. The relative paucity of species on the lower eastern slope is most likely a result of the much drier conditions there.

Microhabitat and Diel Activity

Observations of the frogs of the Cordillera de Huancabamba reveal many differences in resource utilization by period of activity and microhabitat preferences. The three dendrobatids are the only diurnal species. *Epipedobates tricolor* and *Colostethus elachyhistus* are terrestrial and inhabit riparian situations at low elevations; *Colostethus sylvaticus* is the high-altitude equivalent. The only other species associated with streams are *Centrolene buckleyi*, which is predominantly arboreal and nocturnal, and *Telmatobius ignavus*, which is aquatic. Most individuals of all other anurans (species of *Eleutherodactylus*, *Gastrotheca*, *Phrynopus*, and *Phyllonastes*) were active at night. The two species of *Phrynopus* and one species of *Phyllonastes* are terrestrial. With the exception of the terrestrial *Eleutherodactylus lymani* at lower elevations on the western slope, all *Eleutherodactylus* are arboreal. Two species (*E. cajamarcensis* and *E. colodactylus*) at high elevations on the eastern slope utilize arboreal bromeliads as diurnal retreats. The other arboreal nocturnal *Eleutherodactylus* seem to be separated along an altitudinal gradient. The greatest number of syntopic *Eleutherodactylus* is four at 2770 m on the western slope—*E. cryptomelas*, *E. phoxocephalus*, *E. rhodoplichus*, and *E.* sp. Also, four species (*E. ceuthospilus*, *E. lymani*, *E. sternothylax* and *E. wiensi*) were found at 1735 m on the western slope, but one of these (*E. lymani*) is terrestrial. The species of *Gastrotheca* are nocturnal and primarily arboreal; *G. galeata*, which also occurs on the ground at low elevations on the western slope, is replaced by *G. lateonota* in humid montane forest at higher elevations, whereas *G. monticola* occurs in dry tropical forest on the eastern slope.

From these limited observations only coarse-grained differences in resource utilization can be recognized on the basis of period of activity and microhabitat preference. The differences seem to be primarily at the generic level. *Colostethus* and *Epipedobates* are diurnal and riparian; *Phrynopus* and *Phyllonastes* are nocturnal and terrestrial, and *Eleutherodactylus* (with the exception of *E. lymani*), *Centrolene*, and *Gastrotheca* are nocturnal and arboreal, whereas *Telmatobius* is aquatic. Species within a genus are either sufficiently separated by altitudinal replacement, size, reproductive mode (see next sections), or coexist at a given altitude by fine-grained ecological differences that we failed to detect.

Interspecific Size Differences and Sexual Dimorphism

Within habitats on the Cordillera de Huancabamba, interspecific differences exist in size among most anurans (Table 1). In the lower tropical dry forest of the western slope, the dendrobatids, *Colostethus elachyhistus* and *Epipedobates tricolor*, are nearly the same size and seem

Table 1. Size and sexual dimorphism in anurans from the Cordillera de Huancabamba. Sizes are snout-vent lengths are given as ranges followed by $\bar{X} \pm 1$ SD.

Taxon	Males			Females			Females/ Males
	n	Range	($\bar{X} \pm 1$ SD)	*n*	Range	($\bar{X} \pm 1$ SD)	
Centrolene buckleyi[1]	22	27.9 –33.0	(30.1 ± 1.3)	20	28.3 –34.9	(31.1 ± 1.6)	1.03
Colostethus elachyhistus	23	15.4 –20.2	(18.3 ± 1.3)	23	18.1 –23.4	(21.2 ± 1.5)	1.16
Colostethus sylvaticus	8	16.7 –25.7	(23.6 ± 2.9)	19	22.6 –30.4	(28.6 ± 1.8)	1.21
Epipedobates tricolor	5	16.5 –18.4	(17.5 ± 0.8)	6	16.3 –19.8	(18.8 ± 1.3)	1.07
Gastrotheca galeata	5	41.5 –46.0	(44.0 ± 1.9)	8	48.5 –59.4	(52.0 ± 3.9)	1.18
Gastrotheca lateonota	0	—	—	12	54.5 –63.7	(59.4 ± 3.3)	—
Gastrotheca monticola	5	51.1 –59.2	(53.9 ± 3.1)	4	56.9 –67.6	(61.5 ± 4.8)	1.14
Eleutherodactylus cajamarcensis	5	22.6 –25.9	(24.7 ± 1.4)	14	27.0 –32.0	(29.2 ± 1.6)	1.18
Eleutherodactylus ceuthospilus	35	19.0 –25.8	(21.3 ± 1.5)	8	23.5 –26.7	(25.2 ± 1.3)	1.18
Eleutherodactylus colodactylus	15	15.8 –20.0	(17.8 ± 1.1)	1	20.7	—	1.16
Eleutherodactylus cryptomelas[2]	4	28.2 –30.2	(29.2)	1	38.6	—	1.32
Eleutherodactylus lymani	3	40.1 –46.1	(42.1 ± 3.4)	3	53.9 –66.7	(61.3 ± 6.6)	1.46
Eleutherodactylus phoxocephalus[2]	18	22.3 –29.9	(26.1)	10	29.6 –38.4	(34.0)	1.30
Eleutherodactylus rhodoplichus	17	21.8 –28.9	(25.8 ± 1.8)	4	30.1 –34.2	(32.5 ± 2.1)	1.26
Eleutherodactylus sternothylax	39	18.3 –29.1	(24.2 ± 2.4)	6	28.3 –36.7	(32.1 ± 3.1)	1.33
Eleutherodactylus wiensi	6	27.8 –33.0	(30.7 ± 2.3)	1	37.0	—	1.21
Eleutherodactylus sp.	1	20.4	—	0	—	—	—
Phrynopus nebulanastes	20	27.9 –36.4	(33.7 ± 2.4)	14	32.9 –42.1	(37.8 ± 2.6)	1.12
Phrynopus parkeri	39	21.9 –27.4	(24.0 ± 1.2)	39	28.2 –35.1	(31.9 ± 1.0)	1.33
Phyllonastes heyeri[3]	5	12.9 –14.1	(13.8 ± 0.2)	4	13.1 –15.9	(14.6 ± 0.6)	1.06
Telmatobius ignavus	1	75.4	—	4	70.5 –80.3	(75.8 ± 4.1)	1.01

[1]Various localities in Ecuador; specimens in KU collection.
[2]From Lynch (1979).
[3]From Lynch (1986).

to occupy the same riparian microhabitat. The terrestrial *Eleutherodactylus lymani* is the largest member of the genus in the region and shows the greatest degree of sexual dimorphism with females much larger than males; the arboreal *Eleutherodactylus wiensi* is intermediate in size between *E. lymani* and the dendrobatids (Fig. 19).

In the humid montane forest on the western slope (1700–3000 m), the six species of arboreal *Eleutherodactylus* do not differ greatly in size. The single specimen of *Eleutherodactylus* sp. is the smallest and males of *E. ceuthospilus* are not much larger. Females of *E. ceuthospilus* are about the same size as the males of *E. phoxocephalus*, *E. rhodoplichus*, and *E. sternothylax*, all of which are all about equal in size and have about the same degree of sexual dimorphism. *Eleutherodactylus cryptomelas* is slightly larger than any other *Eleutherodactylus* in the humid montane forest. Although females of the terrestrial *Phrynopus nebulanastes* are about the same size as females of *Eleutherodactylus cryptomelas*, the males are larger than males of any of the species of *Eleutherodactylus*. The two species of *Gastrotheca* are much larger than the other terrestrial or arboreal frogs in the humid montane forest; females of *G. lateonota* are much larger than those of *G. galeata*. *Phyllonastes heyeri* is the smallest anuran in the entire region.

Of the species at the summit, *Colostethus sylvaticus*, *Eleutherodactylus cajamarcensis*, and *Phrynopus parkeri* are all about equivalent in size; *Eleutherodactylus colodactylus* is smaller and *Centrolene buckleyi* is larger. The aquatic *Telmatobius ignavus* is the largest frog in the cordillera. The species at low elevations on the eastern slope differ widely in size; *Gastrotheca monticola* is very large, whereas *C. elachyhistus* is small.

Within habitats, size differences generally exist among species; however, there are groups of similar-sized species within each habitat, except for the tropical dry forest of the eastern slope. In the tropical dry forest of the western slope, *Colostethus elachyhistus* and *Epipedobates tricolor* are nearly the same size. Three species of *Eleutherodactylus* (*E. phoxocephalus*, *E. rhodoplichus*, and *E. sternothylax*) in the humid montane forest on the western slope are similar in size; however, they differ in altitudinal distribution within the humid montane forest (*E. sternothylax* 1735–1800 m, *E. phoxocephalus* 1850–2770 m, *E. rhodoplichus* 2770–3050 m). At high elevations in humid montane forest, *C. sylvaticus*, *E. cajamarcensis*, and *P. parkeri* are all similar in size, but they differ in microhabitats—riparian, arboreal, and terrestrial, respectively.

Reproductive Modes

The distinct habitats across the cordillera reflect the underlying gradient of moisture and altitude. Anuran amphibians are intimately dependent on

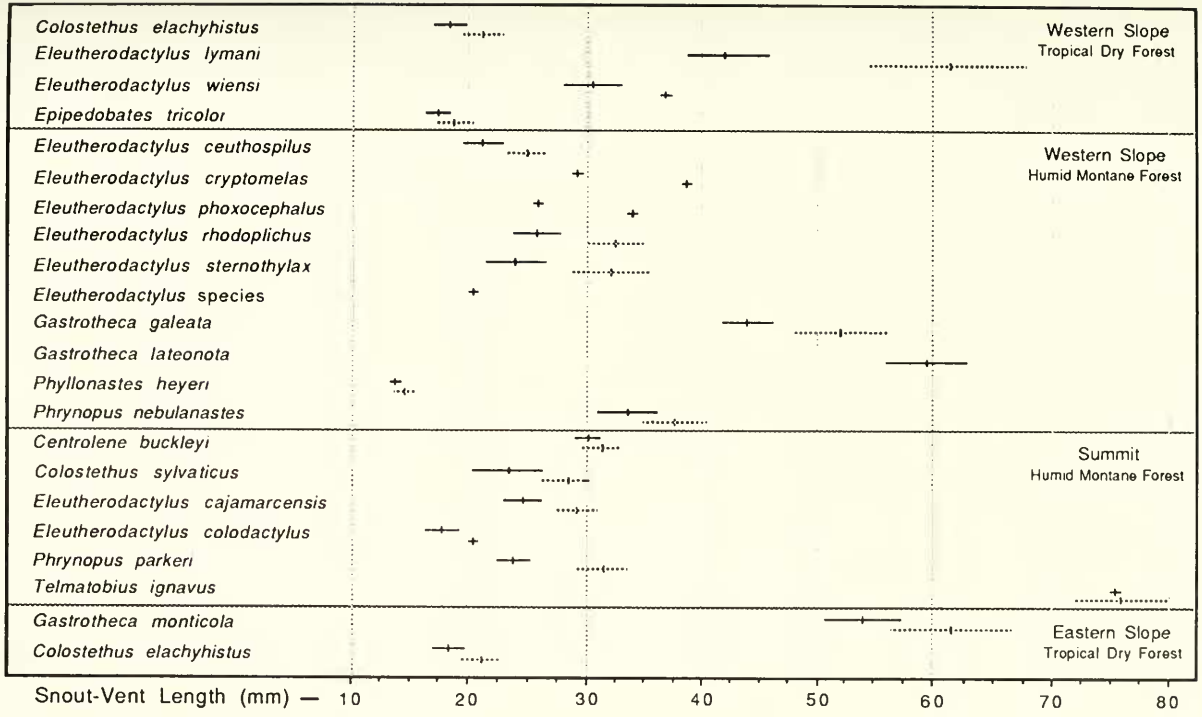

Fig. 19. Snout-vent lengths (±1 SD) of anurans in the Cordillera de Huancabamba by habitat. (Solid lines are males and dotted lines are females; data from Table 1.)

moisture for survival and reproduction; thus it is not surprising to observe a correspondence between habitats and diversity in reproductive modes. The most common mode of reproduction among the frogs of the cordillera is that of terrestrial eggs with direct development, as exhibited by all species of *Eleutherodactylus*, *Phrynopus*, and *Phyllonastes* (13 species). These species are found predominantly in the humid montane forest (1700–3000 m, 8 species) with only two in the lower dry tropical forest (< 1700 m), and three mostly above 3000 m. Because successful development of terrestrial eggs depends on ambient moisture, it is clear why the preponderance of these species is in the humid montane forest.

The three species of dendrobatids lay terrestrial eggs, but the hatchling tadpoles are transported to, and develop in, water. These species must remain near streams, especially in the low tropical dry forest, where this is the only water available. Similarly, *Centrolene* and *Telmatobius* lay their eggs on vegetation above, or in, water, respectively, and are similarly restricted.

The three species of *Gastrotheca* are egg brooders; females carry eggs in a dorsal pouch and deposit tadpoles in ponds (*G. lateonota* and *G. monticola*) or the eggs undergo direct development (*G. galeata*). Egg brooding permits more freedom from ties to standing bodies of water. This allows *G. monticola* to exist in tropical dry forest on the eastern slope.

Summary of Ecological Distribution

In order to ascertain ecological similarities and differences among anuran species in the Cordillera de Huancabamba and to evaluate the relative importance of habitat, microhabitat, diel activity, body size, and reproductive mode on the ecological distribution of these frogs, data on these parameters (Table 2) were subjected to cluster analysis. The codes for habitat are ordered with increasing moisture and altitude. The codes for microhabitat are ordered by increasing terrestriality, and those for reproduction generally follow a decrease in dependency on water and increased specialization. Therefore, distances generated by the cluster analysis approximate degrees of ecological difference. However, the results are presented simply as a descriptive aid, and are not meant to be interpreted as strict quantitative measures.

Seven species groups are recognized on the basis of ecological similarity. In terms of the ecological parameters included in Table 2, the most different species ecologically is *Telmatobius ignavus*, the largest and the only totally aquatic frog of the region and the only species that deposits eggs in streams, where the tadpoles also develop. The dendrobatids (*Colostethus sylvaticus*, *C. elachyhistus*, and *Epipedobates tricolor*) form a distinctive group in being riparian, diurnal, and depositing eggs on land and carrying

Table 2. Data matrix for analyses of ecological distribution of anurans.*

Taxon	Parameter				
	Diel activity	Habitat	Micro-habitat	Repro. mode	Size
Centrolene buckleyi	1	5	4	3	33.9[1]
Colostethus elachyhistus	2	2	2	2	21.8
Colostethus sylvaticus	2	4	2	2	28.1
Epipedobates tricolor	2	1	2	2	19.1
Gastrotheca galeata	1	3	4	6	52.7
Gastrotheca lateonota	1	3	4	5	56.5
Gastrotheca monticola	1	1	4	5	63.4
Eleutherodactylus cajamarcensis	1	5	4	4	29.0
Eleutherodactylus ceuthospilus	1	3	4	4	26.3
Eleutherodactylus colodactylus	1	4	4	4	20.4
Eleutherodactylus cryptomelas	1	3	4	4	34.4[2]
Eleutherodactylus lymani	1	2	3	4	56.4
Eleutherodactylus phoxocephalus	1	3	4	4	34.2[2]
Eleutherodactylus rhodoplichus	1	4	4	4	31.6
Eleutherodactylus sternothylax	1	3	4	4	32.9
Eleutherodactylus wiensi	1	2	4	4	35.0
Eleutherodactylus sp.	1	3	4	4	20.4
Phrynopus nebulanastes	1	3	3	4	39.3
Phrynopus parkeri	1	4	3	4	28.0
Phyllonastes heyeri	1	4	3	4	15.0[3]
Telmatobius ignavus	1	4	1	1	77.9

*Size is the average of snout-vent length of largest male and largest female. All other parameters are coded—Diel activity: 1 = nocturnal; 2 = diurnal. Habitat: 1 = tropical dry forest; 2 = tropical dry forest and humid montane forest; 3 = humid montane forest; 4 = humid montane forest and upper montane forest; 5 = upper montane forest. Microhabitat: 1 = aquatic; 2 = riparian; 3 = terrestrial; 4 = arboreal. Reproductive mode: 1 = eggs and tadpoles in streams; 2 = eggs on land, tadpoles carried to streams; 3 = eggs on leaves, tadpoles in streams; 4 = eggs on land undergoing direct development; 5 = eggs brooded by female; tadpole in ponds; 6 = eggs brooded by female and undergoing direct development.

[1]Various localities in Ecuador; specimens in KU collection.

[2]From Lynch (1979).

[3]From Lynch (1986).

tadpoles to streams. The three species of *Gastrotheca* are larger than most other frogs in the cordillera, but they differ principally in that females brood eggs. *Gastrotheca monticola* is grouped separately from *G. lateonota* and *G. galeata* because it inhabits tropical dry forest, in contrast to the humid montane forest.

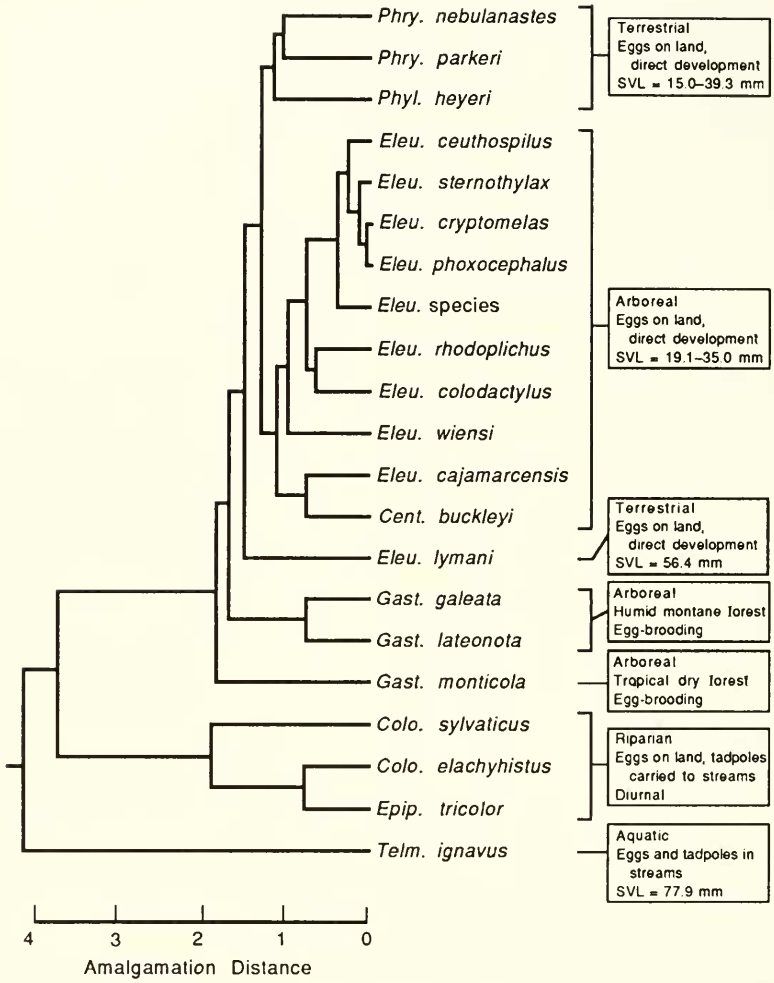

Fig. 20. Phenogram of ecological similarity from cluster analysis of ecological data in Table 2.

Eleutherodactylus lymani is placed in its own group because it differs from all other leptodactylids in being much larger (except for *Telmatobius ignavus*) and from other *Eleutherodactylus* because it is terrestrial. *Eleutherodactylus lymani* is no more similar to species of *Gastrotheca*, the other large frogs of the cordillera, than other *Eleutherodactylus* because it is terrestrial and deposits eggs directly on land where they undergo direct development. All remaining *Eleutherodactylus* and *Centrolene buckleyi* form the largest group. All of these species are small to medium-sized

arboreal frogs; all deposit eggs on land where they undergo direct development except *Centrolene buckleyi*, which deposits eggs on leaves over streams where the tadpoles develop. Species in the final group, consisting of *Phrynopus nebulanastes*, *P. parkeri*, and *Phyllonastes heyeri*, are similar in size and reproductive mode to the *Eleutherodactylus* group, but differ in being terrestrial.

The ecological data reveal that the anurans of the Cordillera de Huancabamba partition each habitat. Within the western slope dry tropical forest, only two species are from the same ecological group; *Colostethus elachyhistus* and *Epipedobates tricolor* show no apparent ecological differences. *Eleutherodactylus wiensi* and *E. lymani* are larger, nocturnal, and have direct development; however, *E. lymani* is much larger and terrestrial, whereas *E. wiensi* is arboreal. Thus, with the exception of the dendrobatids, the species in the tropical dry forest are segregated by size and microhabitat.

In the humid montane forest of the western slope, the two species of *Gastrotheca*, which are separated altitudinally, are large and brood eggs; thus, they differ from the other frogs (all leptodactylids) there. *Phyllonastes heyeri*, the smallest frog in the region, and the larger *Phrynopus nebulanastes* differ from other anurans in the humid montane forest by being terrestrial. Among the six species of *Eleutherodactylus* in the humid montane forest, *E. ceuthospilus* and *E. sternothylax* (1735–1840 m) are separated altitudinally from *E. cryptomelas*, *E. phoxocephalus*, *E. rhodoplichus*, and *E.* sp. (1850–3050 m). Of the latter four species, the altitudinal overlap by *E. phoxocephalus* and *E. rhodoplichus* with the other two species is slight, and *E.* sp. is much smaller than the other three. In the humid montane forest, the *Gastrotheca* differ from other anurans in reproductive mode; secondarily, the species differ from one another in size. *Phyllonastes* and *Phrynopus* differ from the other anurans in microhabitat and from one another in size. Size and microhabitat set the species of *Eleutherodactylus* apart from the other anurans, and the species differ from one another in altitudinal distribution and in size.

Among species at the summit, *Colostethus sylvaticus*, *Phrynopus parkeri*, and *Telmatobius ignavus* are in different ecological groups. The latter is unique in microhabitat, size, and reproductive mode; *C. sylvaticus* differs in diel activity, size, and reproductive mode, and *P. parkeri* differs in microhabitat. *Eleutherodactylus cajamarcensis*, *E. colodactylus*, and *Centrolene buckleyi* differ from the other species in microhabitat and from each other in size.

The two species found in the lowland tropical dry forest of the eastern slope, *Gastrotheca monticola* and *Colostethus elachyhistus*, differ widely in all the ecological parameters examined.

At generic and suprageneric levels, resource partitioning within habitats

in the region is achieved by differences in microhabitat, diel activity, reproductive mode, and size. Except for the dendrobatids, which are diurnal and myrmecophagous, size of the frogs is probably correlated with the size of prey eaten. Congeners within habitats differ mostly in size and altitudinal distribution. The latter possibly is correlated with thermal or moisture tolerances or with fine-grained microhabitat differences not detected by us.

BIOGEOGRAPHY

The region of the Huancabamba Depression has been regarded as a major biogeographic discontinuity in the distributions of Andean plants and animals. This has been documented for various groups of plants by Simpson (1975), for birds by Vuilleumier (1969) and Parker et al. (1985), for amphibians and reptiles by Duellman (1979), and for lizards of the genus *Stenocercus* by Cadle (1991). Therefore, a biogeographic analysis of the anuran fauna of the Cordillera de Huancabamba in the midst of the Huancabamba Depression is especially significant. Ideally, such an analysis would rely on area cladograms resulting from phylogenetic analyses of all component taxa and their relatives. However, phylogenetic analyses are unavailable for most of the taxa; thus, we are limited to analyzing patterns of distribution.

Distribution Patterns

Of the 21 species of anurans inhabiting the Cordillera de Huancabamba, 10 are known only from that cordillera (of these, *Colostethus sylvaticus* also occurs in the cordillera to the east of the Río Huancabamba). The other 11 species also occur in one or more other areas in northern Peru and southern Ecuador (Table 3, Fig. 1). These other five areas represent eastern and western slopes of the Andes and an inter-Andean basin; they are as follow.

Abra de Zamora: A ridge reaching an elevation of 2800 m in the Cordillera Oriental, 15 km (by road) east of Loja, Provincia Loja, including the eastern slopes in Provincia Zamora-Chinchipe, Ecuador.

Cordillera Central, Peru: The northern part of the Andes in Departamento Amazonas, Peru.

Cordillera Occidental, Peru: The northern Andes in Departamento Cajamarca, Peru.

Loja Basin, Ecuador: An inter-Andean basin at an elevation of 2150 m in Provincia Loja in southern Ecuador.

Pacific slopes of Ecuador: The western slopes of the Cordillera Occidental in provincias El Oro and Azuay south of the Río Jubones, Ecuador.

Table 3. Distribution of anurans from the Cordillera de Huancabamba in other regions.

Taxon	Regions				
	PSE	AZE	LBE	COP	CCP
Centrolenidae:					
Centrolene buckleyi	–	+	–	–	–
Dendrobatidae:					
Colostethus elachyhistus	–	–	+	–	–
Colostethus sylvaticus	–	–	–	–	+
Epipedobates tricolor	+	–	–	–	–
Hylidae:					
Gastrotheca galeata	–	–	–	–	–
Gastrotheca lateonota	–	–	–	–	–
Gastrotheca monticola	+	–	+	–	+
Leptodactylidae:					
Eleutherodactylus cajamarcensis	–	–	+	–	–
Eleutherodactylus ceuthospilus	–	–	–	+	–
Eleutherodactylus colodactylus	–	+	–	–	–
Eleutherodactylus cryptomelas	–	+	–	–	–
Eleutherodactylus lymani	+	–	+	–	–
Eleutherodactylus phoxocephalus	+	–	–	–	–
Eleutherodactylus rhodoplichus	–	–	–	–	–
Eleutherodactylus sternothylax	–	–	–	–	–
Eleutherodactylus wiensi	–	–	–	–	–
Eleutherodactylus sp.	–	–	–	–	–
Phrynopus nebulanastes	–	–	–	–	–
Phrynopus parkeri	–	–	–	–	–
Phyllonastes heyeri	–	+	–	–	–
Telmatobius ignavus	–	–	–	–	–

*AZE = Abra de Zamora, Ecuador; CCP = Cordillera Central, Peru; COP = Cordillera Occidental, Peru; LBE = Loja Basin, Ecuador; PSE = Pacific slopes of Cordillera Occidental, Ecuador (see Fig. 1).

The four species shared with the Abra de Zamora (*Centrolene buckleyi*, *Eleutherodactylus colodactylus*, *E. cryptomelas*, and *Phyllonastes heyeri*) and three of the four species shared with the Pacific slopes in Ecuador (*Epipedobates tricolor*, *Eleutherodactylus lymani*, and *E. phoxocephalus*) reach the southern limits of their distributions in the Cordillera de Huancabamba. *Eleutherodactylus colodactylus* and *E. cryptomelas* are

known from several localities at elevations of 2100–3100 m in the Cordillera Oriental in southern Ecuador (Lynch, 1979) and *Phyllonastes heyeri* is known only from a single locality on the eastern slope of the Andes in southern Ecuador (Lynch, 1986); *E. phoxocephalus* is widespread at elevations of 2000–3000 m on the Pacific slopes of the Cordillera Occidental in Ecuador (Lynch, 1979). Likewise, *Centrolene buckleyi* is widespread at elevations of 2000–3000 m in the Andes of Ecuador, Colombia, and Venezuela (Lynch and Duellman, 1973). *Eleutherodactylus lymani* occurs in semiarid valleys and on the lowlands at elevations of 690–2500 m (Lynch, 1979), and *Epipedobates tricolor* also occurs in semiarid valleys and on the lowlands at elevations of 20–1690 m.

Eleutherodactylus lymani also occurs in the semiarid Loja Basin, where it is sympatric with *Colostethus elachyhistus*, *Eleutherodactylus cajamarcensis*, and *Gastrotheca monticola* (Edwards, 1971; Lynch, 1969; Duellman and Hillis, 1987). All of these species occur in tropical dry forest at elevations below 1700 m on the western slopes and 1840 m on the eastern slopes of the Cordillera de Huancabamba, except *E. cajamarcensis*, which occurs on the upper western slopes of the cordillera. The latter species also is shared with the Cordillera Occidental in Peru. The only other species shared with that cordillera is *Eleutherodactylus ceuthospilus*.

Gastrotheca monticola is widespread in southern Ecuador and northern Peru, where it occurs at elevations of 1000–3350 m in semiarid areas (e.g., Loja Basin and Huancabamba Valley) and in humid montane forests on the Pacific slopes of the Cordillera Occidental in southern Ecuador and in the Cordillera Central in northern Peru (Duellman and Hillis, 1987). This species and *Eleutherodactylus cajamarcensis* are the only two species that occur in the Cordillera de Huancabamba and to the north and south of that cordillera. *Eleutherodactylus ceuthospilus* is the only species that reaches its northern distribution limits in the Cordillera de Huancabamba, whereas eight species (*Centrolene buckleyi*, *Colostethus elachyhistus*, *Epipedobates tricolor*, *Eleutherodactylus colodactylus*, *E. cryptomelas*, *E. lymani*, *E. phoxocephalus*, and *Phyllonastes heyeri*) reach their southern distribution limits in that cordillera. Of these eight species, five are inhabitants of cloud forest, and three live in dry forest.

Phylogenetic Analyses

No phylogenetic analyses are available for *Centrolene*, *Colostethus*, *Epipedobates*, *Eleutherodactylus*, *Phyllonastes*, or *Telmatobius*. *Gastrotheca monticola* is the southernmost member of the *Gastrotheca plumbea* group, which occurs principally in Colombia and Ecuador (Duellman and Hillis, 1987; Duellman et al., 1988). Immunologically, *Gastrotheca galeata* and *G. lateonota* are members of the *Gastrotheca*

marsupiata group, which, except for the Ecuadorian *G. pseustes*, is distributed in the Andes from the Huancabamba Depression southward. These relationships are supported by osteological data (Trueb and Duellman, 1978; Duellman and Trueb, 1988).

According to the phylogenetic analysis of *Phrynopus* presented by Cannatella (1984), *P. nebulanastes* and *P. parkeri* form an unresolved polytomy with *P. flavomaculatus* from the Abra de Zamora in Ecuador and *P. lucida* from the central part of the Cordillera Oriental in Peru. These species form a clade in the midst of other Peruvian and Ecuadorian species. Thus, the phylogenetic arrangement of *Phrynopus* contributes little to our understanding of biogeography.

Comparisons with Other Cordilleras

Herpetological collections are available from three isolated cordilleras to the northeast of the Cordillera de Huancabamba. These are the Cordillera del Cóndor and Cordillera de Cutucú to the east of the Cordillera Oriental of the Andes in southern Ecuador and the Cordillera Colán in the eastern part of the Huancabamba Depression in northern Peru (Fig. 1). No species are shared between the Cordillera de Huancabamba and any of these isolated cordilleras. Of the 24 species of anurans known from the Cordillera de Cutucú, two (*Atelopus halihelos* and *Eleutherodactylus ganonotus*) are endemic and 13 are shared with the Cordillera del Cóndor, which has three endemic species—*Colostethus mystax*, *C. shuar*, and *Ischnocnema simmonsi* (Duellman and Lynch, 1988). A small collection of amphibians made in the Cordillera Colán by ornithologists from Louisiana State University contains many new species, only two of which have been named—*Gastrotheca abdita* (Duellman, 1987) and *Telmatobius colanensis* (Wiens, 1992). Other species from the Cordillera Colán include one new species of *Atelopus*, one of *Cochranella*, and three of *Eleutherodactylus*.

Each of these cordilleras has its peculiarities. For example, there are no centrolenids reported from the Cordillera del Cóndor or the Cordillera de Cutucú and no dendrobatids from the Cordillera Colán. The apparent absence of *Atelopus* from the Cordillera de Huancabamba is puzzling in that the genus is represented in all of the other highland areas. Eleutherodactyline frogs (*Eleutherodactylus*, *Ischnocnema*, *Phrynopus*, and *Phyllonastes*) are especially numerous in these cordilleras—13 in Huancabamba, 12 in Cutucú, 10 in Cóndor, and at least three in Colán.

General Distribution Patterns

Frogs of the genera *Centrolene*, *Colostethus*, *Eleutherodactylus*, and *Phrynopus* are more speciose in the humid Andes to the north of the Huancabamba Depression than in the drier Andes to the south of the

depression, where most species in these genera are restricted to the humid Andean slopes of the Andes. Of the four species of *Phyllonastes*, one is Amazonian, one is restricted to the Cordillera Central in northern Peru, one is on the Amazon slopes of the Ecuadorian Andes, and *P. heyeri* occurs in the latter and in the Cordillera de Huancabamba (Duellman, 1991). As noted previously, the Huancabamba Depression is a major break in the distributions of members of two species groups of *Gastrotheca;* only one species of the *Gastrotheca marsupiata* group occurs to the north of the depression and only one species of the *Gastrotheca plumbea* group occurs to the south of the depression (Duellman et al., 1988). Frogs of the genus *Telmatobius* belong to a Patagonian-southern Andean faunal element (Duellman, 1979); only three of more than 30 species occur to the north of the Huancabamba Depression (Trueb, 1979).

Biogeographic Summary

Lying as it does in the middle of the Huancabamba Depression, the Cordillera de Huancabamba supports an anuran fauna composed of taxa having affinites with species in the Andes to the north and to the South of the depression. Nine of the 21 species certainly seem to have northern affinites, and three definitely have southern affinities. Seven of the remaining nine species are endemic to the cordillera and are of unknown affinities. Until the phylogenetic relations of many of the taxa have been ascertained, refinement of the biogeographic analysis is not possible. Furthermore, additional cordilleras need to be sampled. If other uncollected ranges are as rich in undescribed species as the Cordillera de Huancabamba and the Cordillera Colán, the highlands in the Huancabamba Depression will be noteworthy for their large, mostly endemic anuran faunas.

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